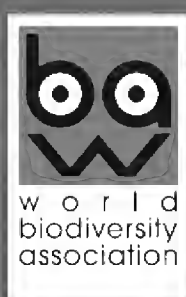


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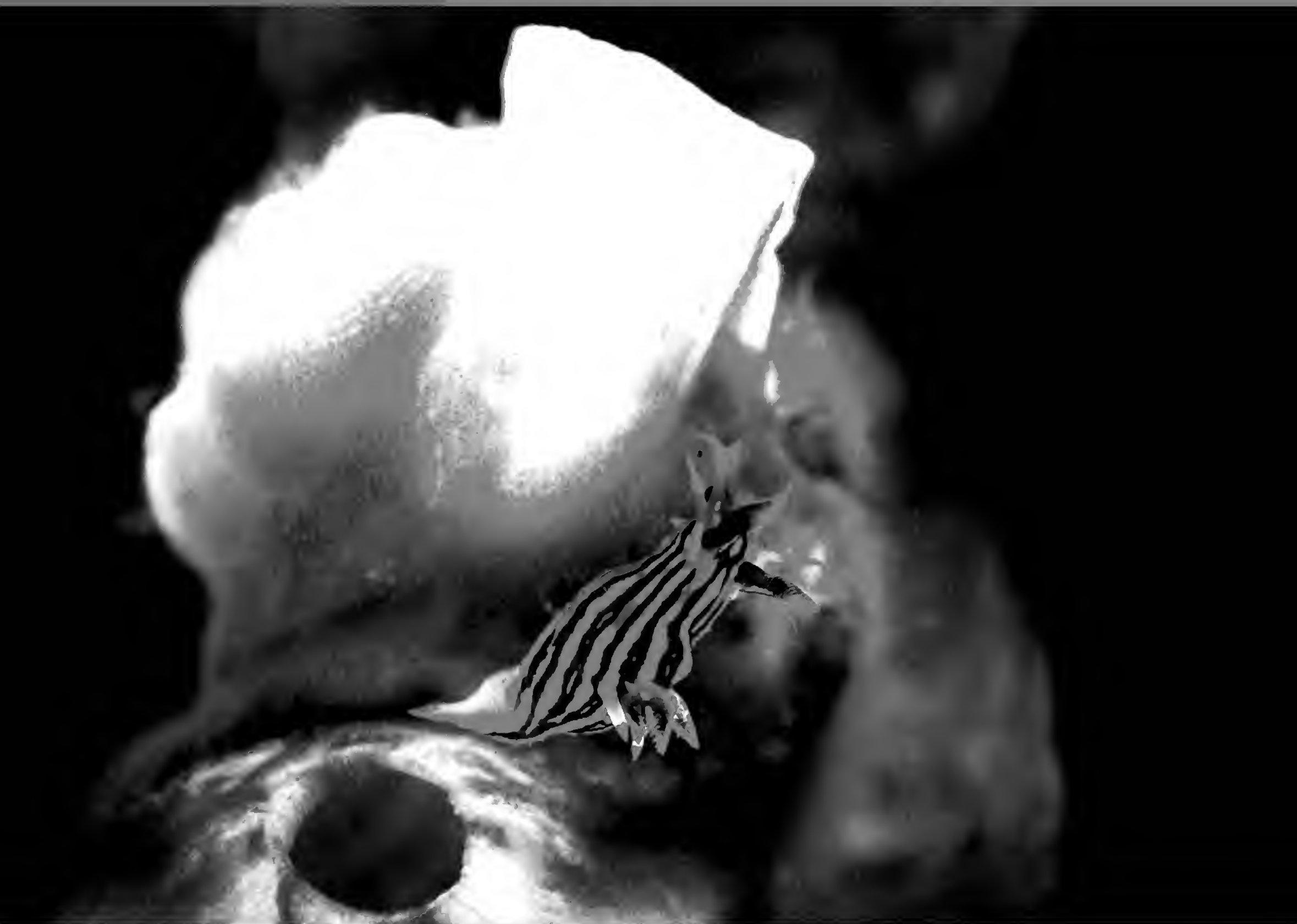
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*Polycera quadrilineata* (O. F. Müller, 1776) - Eastern Sicily, Mediterranean Sea

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***Polycera quadrilineata* (O.F. Müller, 1776) (Gastropoda Polyceridae).** Order Nudibranchia (Mollusca, Opisthobranchia). Nudibranchs are commonly known as "sea slugs" because they are not shelled molluscs. The evolution of the shell in gastropods followed a complexity plan of development, starting from simply low spiral, patelliform structures to highly twisted shells, the most safety house where a soft-body animal could hide from predators. How could shells be more efficient? After the "invention" of the shell, gastropods - which became heavy and slow - started to produce a thin shell. Increasing mobility conducted to shell reduction and this latter required a new plan of defense from predators. Probably around 3 or 4 hundreds of years ago, nudibranchs evolved from shelled molluscs and diversified. What is the successful of this new branch of gastropods due to? Toxicity or simply disgust to predators. This condition was reached by nudibranchs in two different ways. Some accumulate chemical active molecules throughout their tissues from the natural host upon which they feed, thus resulting venomous or stodgy. Some others build an internal equipment of spicules, which make them very hard to eat. How to inform their potential predators of their dangerous internal items? Nudibranchs are very beautiful marine organisms, showing delicate external soft parts and spectacular colors, often eomparable to butterflies. The reason of these showy colorations is the aposematic message; warning colorations mean: "I am venomous" so that predators immediately learn it is better to avoid these striking animals.

The photograph shows a specimen of *P. quadrilineata* crawling on an ascidian looking for some encrusting bryozoans to eat (Summer 2004, Riposto, Catania, Eastern Sicily) (cover photo by Danilo Scuderi).

**Danilo Scuderi.** Via Mauro de Mauro 15b, Belpasso, Catania; e-mail: danscu@tin.it

## Nesting of the Black Stork *Ciconia nigra* Linnaeus, 1758 (Aves Ciconiidae) in the Fiumara Vittravo Valley (Calabria, Italy)

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### ABSTRACT

The Fiumara Vittravo Valley in the province of Crotone in Italy, is a Site of National Interest for its rich biodiversity and peculiar habitat, and also a strategic area for the nesting of Black Stork, *Ciconia nigra* Linnaeus, 1758 (Aves Ciconiidae). The river morphology, the harshness of this wild territory, the luxuriant vegetation, the presence of a hydrographic network rich of trophic resources and the crucial position along the migratory routes, are fundamental for the reproductive biology and the evolution of this species. This work will expose the results of the monitoring activities that were carried out in 2015 by which it was possible to document the Black Stork nesting on rocky areas in the valley of Fiumara Vittravo. The ecological importance of the area is strongly in need of greater scientific attention and a suitable site preservation in order to favor the population increment of the Black Stork also in Calabria, where the active reproductive population was present only until 2001. The results are in evident countertrend with respect to older statistical data, which provide negative and sparse data for black stork presence in the “Alto Crotonese” region.

### KEY WORDS

*Ciconia nigra*; Crotone; Calabria; nesting site.

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### INTRODUCTION

The Black Stork, *Ciconia nigra* Linnaeus, 1758 (Aves Ciconiidae) is a bird with a wide territorial distribution. Its nesting area goes from Spain to Sachalin island between the 35° and 60° North parallel, with a separate population nesting in South Africa (Del Hoyo et al., 1992). The species, having a palearctic afro-tropical chorology, is very rare in western Europe, where it has suffered from drastic reduction with a complete disappearance in some states due to the destruction of its natural habitat. In Italy, the black stork is a migrating nesting species rarely wintering. Its biological characteristic

is of long range flyer, able to travel over large portions of the sea, allowing it to migrate from wintering zones to nesting areas travelling for thousands of kilometers.

The populations move along not well defined routes, crossing the Mediterranean sea on a wide frontline. Some groups travel through the Strait of Gibraltar, others through the Red Sea along the Suez Canal to the Caucasian regions, others from the Black Sea go through the Bosphorus. One group crosses the eastern Mediterranean from Peloponnese partially exploiting the bridge formed by the Egeo islands. A small group proceeds along the Sicily channel and the Italian peninsula (Petretti, 1993).

The passage of Black Stork in Calabria is not well documented for the lack of an observation network throughout the territory. Small groups of isolated individuals, observed during the passage, may lead one to think both the Tyrrhenian and Ionic side of Calabria as preferential migratory routes, although the crossing of the Sila plateau cannot be excluded.

In general, the reproduction area of the species should include Eurasia, Southern Africa and Western Spain at the border with Portugal. Isolated populations are also found in central Europe and Balkans. The eastern reproduction area is more continuous including the north-east of Turkey, the Caucasus, and a wide region of Russia. In Italy, the first verified nesting was in 1994 in the natural park of Monte Fenera in the bassa Valsesia in the Piedmont region. In the last years a gradual increment of the number of nesting couples has been observed in several Italian regions with a preference for the southern regions (Bordignon, 2006).

## THE BLACK STORK IN CALABRIA

At the end of the 19th century Lucifero (2003), a man of wide cultural interests, published the first information on the presence of the black stork in Calabria. In that essay the Black Stork is classified as accidental and very rare and its presence was signaled in the area close to Crotone and Isola Capo Rizzuto. In the same essay some statements made by Moschella (in Lucifero, 2003), for the Reggio Calabria province, ensured the presence of the species in that region.

The information was very scarce in the beginning of the century, and only starting from the 1970s, reliable data recorded the species as available in the Calabria region. After 1970 the observations became more frequent with several sightings. In 1994, the Black Stork nested in Calabria, with only one couple bringing four young birds to fly (Bordignon, 1995). The next year another couple brought two to flight. In 1996 no nesting was registered despite the presence of some individuals (G. Rocca personal observation) on the Lese and Neto rivers in the Crotone region. In 1997 only one couple was present bringing two young birds to flight. In the years 1998 and 1999 no nesting was registered but just the presence of isolated individuals on the Lese river (G. Rocca per-

sonal observation). In 2000 only one couple nested in the Crotone region with four flying young birds (Bordignon et al., 2011). In 2001 the same nest was used by a couple for the deposition of four eggs and the flight of four young birds (Rocca, 2002). In the same year a second couple was detected by A. Digiorgio in the same reproduction area. In 2002 the presence of a couple with two immature individuals was registered in the nesting and feeding area. In March 2014, a serious event occurred in one of the most important migratory routes for migrating avifauna. In the core of the Parco Nazionale della Sila an adult black stork was found dead, shot by an unknown poacher in the S. Nicola location in the zone 2 of the park in the Serra Pedace district. In August 2014, during a research campaign, conducted by myself in the valley of Lese river, the presence of an isolated individual was detected. In February 2015, another disappointing event happened on the Amato river near Terzi di Lamezia Terme (Catanzaro) where one specimen was seen with a broken leg in an evident difficult condition but still able to fly (Lega Italiana Protezione Uccelli Sez. Rende, [www.lipurende.it](http://www.lipurende.it)). In the present year an intensive search activity to individuate nesting black storks was successfully accomplished finding a couple regularly nesting on a rock face in the SIN of "Vallone Vittravo".

## SIN (SITE OF NATIONAL INTEREST) "VALLONE VITRAVO"

The Fiumana Vittravo is one of the major rivers of the "Alto Crotonese" district situated in the North East part of the Calabria region, having a major branch length of 43 Km. In its medium highest portion it has a torrential regime, while in the medium part water flows in a deep canyon. Downstream the morphology is like the Calabrian rivers' with a wide bed and holm oaks.

The site "Vallone Vittravo" (IT9300192), belonging to the biogeographic mediterranean region with an abundance of wet fluvial habitat, includes 8 Km of riverbed of this important river extending in its median portion on a surface of about 800 ha.

The area is characterized by a very dense riparian vegetation, with mixed forest of deciduous, sclerophyllous and brushwood, and Mediterranean



low. Ichthyic-fauna based on salmon populates the zones where water flows more rapidly and creates wide and deep potholes, while Cyprinidae stand in the valley areas.

The biotic characterization of Vallone Vittravo was performed since the high naturalistic value of the site makes it a unique habitat for the preservation of important floristic species, peculiar endemic floras and faunas and endangered birds. The geomorphological characteristics of the area, with mighty and inaccessible rock walls, permit the nesting of animal species of the European community interest included into the Attachment 1 of Direttiva "Uccelli" 79/409/CEE as Black Stork, *Ciconia nigra*, nesting area until 2001.

### THE NESTING SITE

In August 2014, on the Lese river, close to the confluence with Neto river, a single individual of black stork was accidentally observed. It was an individual of which it was not possible to obtain any ethological information due to the late reproduction period and the difficulty in finding the feeding sites. In that circumstance the presence of any other individual or nesting site was not detected. This appearance, of great ornithological importance, and related data on spring migration flows pushed us to plan for 2015 a search campaign in the valley of the Fiumara Vittravo, nesting site of the species (Rocca, 2005).

In May 2015 it was identified the pair and the nesting site. The nest was built within a natural cavity at the base of a shelf of rock, on a sandstone rock face in the valley of Fiumara Vittravo. The nest was at an altitude of 370 m on the sea level at the top of the sandstone rock face which is 80 m long with East exposition. The great distance of the nest from the possible observation points, at least 300 m, together with the peculiar conformation of the valley, which barely offer a suitable observation prospective, did not permit to get information on the number of laid eggs. In the first decades of June, two nestlings, apparently one week old, were fed by both parents. In the last decade of July the feeding phase was regularly concluded and the young birds took their first flight.

The nesting site were monitored visually from three observation points at a minimum distance of



Figure 1. Black Stork flying over the Vittravo Valley.

300 m. After hatching, observations were made periodically with short cyclical 10 day visits on the sites in order to avoid disturbing the reproductive cycle of the couple.

### CONCLUSIONS

Nesting of black stork in the valley of Fiumara Vittravo brings the attention of the researchers to a site of greatest importance for the survival of this extraordinary bird. The reproduction success in the Alto Crotonese region shows, in this delicate phase of the geographic expansion of the species, a positive trend in the conquering of the habitats where black stork had disappeared for years. The natural preservation of these fragile and unique ecosystems imposes a collective effort to the scientific community. It should be necessary in the future to continue the monitoring of the site in order to remove or to reduce all the factors (pollution, fire, anthropic impact, etc.) that limit the expansion of the species.

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# The amphioxus *Epigonichthys maldivensis* (Forster Cooper, 1903) (Cephalochordata Branchiostomatidae) larvae in the plankton from Rapa Nui (Chile) and ecological implications

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## ABSTRACT

We report the first record of amphioxus larvae in the plankton from Rapa Nui island (Chile). Zooplankton was sampled using an oblique Bongo net during an oceanographic survey in April and September 2015. A total of four larvae were collected in the coastal area of Rapa Nui in April and 13 in September. The larvae were identified as *Epigonichthys maldivensis* (Forster Cooper, 1903) (Cephalochordata Branchiostomatidae) using both morphological and genetic characters. The water column in this area presented a mean temperature of 21.2°C, a mean salinity of 35.7 ‰ and 4.94 ml/L dissolved oxygen in April, and 20°C and 35.75 ‰ mean salinity in September. Amphioxus have been reported as playing a key role in marine food webs transferring important amounts of microbial production to higher trophic levels, due to this their role in the Rapa Nui plankton and benthos as adults could be interesting because Easter island is located in the oligotrophic gyre of the South Pacific ocean where a microbial trophic web is expected to dominate. This record increases the biodiversity of Rapa Nui plankton and widens the geographic distribution of *E. maldivensis* that was restricted only to the Western and Central Pacific and Indian Ocean.

## KEY WORDS

amphioxus larvae; Pacific Ocean; plankton.

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## INTRODUCTION

The Amphioxus or lancelets (Chordata) comprise the subphylum Cephalochordata (Schubert et al., 2006); which is formed by three genera: *Branchiostoma* Costa, 1834, *Epigonichthys* Peters, 1876 and *Asymmetron* Andrews, 1893 (Kon et al., 2007). The amphioxus are filter-feeding marine organisms that as adults burrow in the sand, gravel or shell deposits in tropical and/or temperate waters around the world ocean (Bertrand & Escriva, 2011). The filtering is performed through jawless ciliated mouths (Vergara et al., 2011).

Amphioxus are found in general in shallow waters close to the shore (0.5 to 40 m depths) and many species prefer habitats of coarse sand and gravel (Desdevises et al., 2011). They live in a variety of coastal habitats, estuaries, coastal lagoons, open coasts and river deltas (Laudien et al., 2007; Chen, 2008). However, little is known about the ecological role of these organisms (Vergara et al., 2011). In addition, some amphioxus have been considered as endangered species (Kubokawa et al., 1998). Environmental factors as temperature and salinity changes are determinant in the life cycle of some amphioxus species (Webb, 1956a; Webb,

1956b; Webb & Hill, 1958). As a consequence, the amphioxus populations migrate between winter and summer (Webb, 1971), and the larvae are described as restricted to waters of high salinity and temperature (Webb & Hill, 1958). The duration and timing of the spawning season varies between species (Stokes & Holland, 1996; Holland, 2011). When the gametes are released in the water, fecundation occurs and the embryos persist in the plankton (Bertrand & Escriva, 2011) until metamorphosis, when they migrate to the sand and become benthic adults.

Some authors have studied the zooplankton and meroplankton around Easter Island (Castro & Landaeta, 2002; Palma & Siva, 2006; Mujica, 2006) most zooplankton results are from CIMAR islands cruise in November 1999. However, there are no records of amphioxus larvae or adults in the area. In this work we describe the presence of amphioxus larvae from Rapa Nui plankton (Chile) for the first time. Larvae were found in stations close to the coast around the island in April and September 2015.

## MATERIAL AND METHODS

Zooplankton samples and hydrographic measurements were gathered in the coastal area of Easter Island or Rapa Nui (27°13' S - 109°37' W), Chile, in April and September 2015. The hydrographic characterization of the water column was done using a set of CTD profiles in both months (Seabird 18).

Zooplankton samples were collected by oblique tows from a depth of 300 m up to the surface, using a Bongo net with 300 µm mesh and 60 cm mouth diameter. The volume of sampled water was estimated using a mechanical flowmeter (General Oceanics) attached to the net. Samples were preserved in 96% ethanol, until laboratory identification and quantification. In these samples seventeen amphioxus larvae were found. Considering that no information about amphioxus larvae morphology is available, three larvae were used to perform the genetic identification. After that a simple morphological description of the larvae is also supplied.

### Genetic identification

Three larvae were used for the genetic analysis. The DNA extraction was conducted using the Qiagen QIAamp kit (Mississauga, Canada). The mitochondrial COI gene was amplified using the protocol and

primers described by Folmer et al. (1994) with 56°C as annealing temperature. Forward and reverse sequencing was performed at Pontificia Universidad Católica de Chile and aligned by eye using the ProSeq v.2.9 software (Filatov, 2002). The haplotype was deposited in Genbank (Accession Number: KU201542). The Blast tool was used to determine similarities with sequences deposited in Genbank.

In order to determine the nucleotide relationship among lancelets, a neighbour-joining based phylogenetic (NJ) analysis was performed using Mega 6.0 software (Tamura et al., 2013). Using a bootstrap of 10,000 replicates, the analysis tested the consistency of each branch in the tree, grouping sequences with similar nucleotide composition. Using this method, unidentified sequence obtained in this study could be grouped with conspecific sampled in other geographical areas.

## RESULTS AND DISCUSSION

A total of 4 amphioxus larvae were found in the coastal area of Rapa Nui in April and 13 in September 2015. The larvae were identified as *Epigonichthys maldivensis* (Forster Cooper, 1903) (Cephalochordata Branchiostomatidae) (Fig. 1). In April, in the south station, larvae were found up to 200 m depth and the abundance was 0.8 individual per 1000 m<sup>3</sup>, while in the south-east station, the abundance of *E. maldivensis* larvae was 2 individuals per 1000 m<sup>3</sup> and were found between 300 m depth and surface. The amphioxus larvae mean abundance in September was 2 individuals per 1000 m<sup>3</sup> and they were found in the south station. The environmental characteristics of the area were mean water temperature of 21.2°C, mean salinity of 35.7 ‰ and 4.94 ml/L dissolved oxygen in April, and 20°C and 35.75 ‰ mean salinity in September.

Genetic identification. One haplotype of 550 bp was obtained for the larvae. The analysis of the COI gene showed a clear relationship of our sequence with *Epigonichthys maldivensis* (Fig. 2). The Blast analysis showed a similarity of 99% with one sequence of *E. maldivensis* (Accession Number: AB110093.1), deposited by Nohara et al. (2005) and obtained from one individual collected in the Kuroshira Island, Japan. Both sequences differ only in 6 bp.

*Epigonichthys maldivensis* is a tropical species whose distribution was restricted only to the Western and Central Pacific and Indian Ocean

(Richardson & McKenzie, 1994; Poss & Boschung, 1996; Lin et al., 2015), the present results expand the geographic range of this species to Rapa Nui island. Lancelets exhibit a week- to month long planktonic larval stage (Wickstead, 1970; Wu et al., 1994; Stokes & Holland, 1996) and in Eastern Island these were present in April and September 2015.

The benthic communities from Rapa Nui are extremely species-poor compared with reefs in the central and western Pacific (Friedlander et al., 2013), the presence of the amphioxus larvae, implies that amphioxus adults probably live in the benthos that would contribute to the benthos species richness. Moreover, anecdotal histories from the local fisherman of Rapa Nui reporting, in some areas and dates, the presence of white filaments like hairs in the bottom, are likely to corroborate our findings; these filaments could be the adult amphioxus. This record increases the biodiversity value of Rapa Nui. In addition, since amphioxus have been reported as playing a key role in marine food webs transferring important amounts of microbial production to higher trophic levels (Chen et al., 2008), their role in the Rapa Nui plankton and benthos as adults could be interesting since Easter island is located in the oligotrophic gyre of the South Pacific ocean where a microbial trophic web is expected to dominate. Finally, new amphioxus genome sequences will be of great importance for comparative genomics at the inter and intra species levels.

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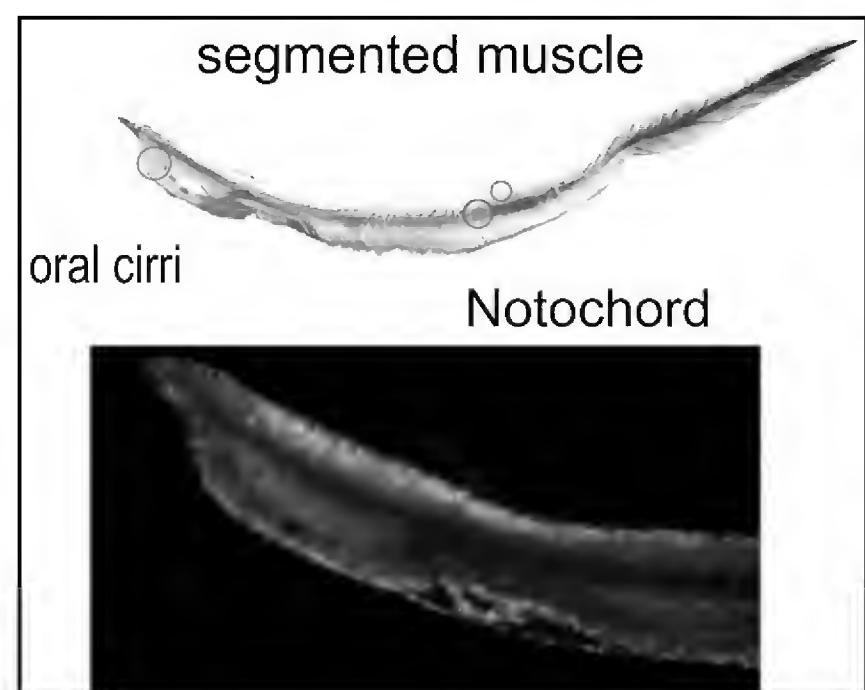


Figure 1. Above: schematic views of the amphioxus larva, basic anatomy the oral cirri, the segmented muscles, and the notochord are signaled. Below: *Epigonichthys maldivensis* larval individual collected from Rapa Nui.

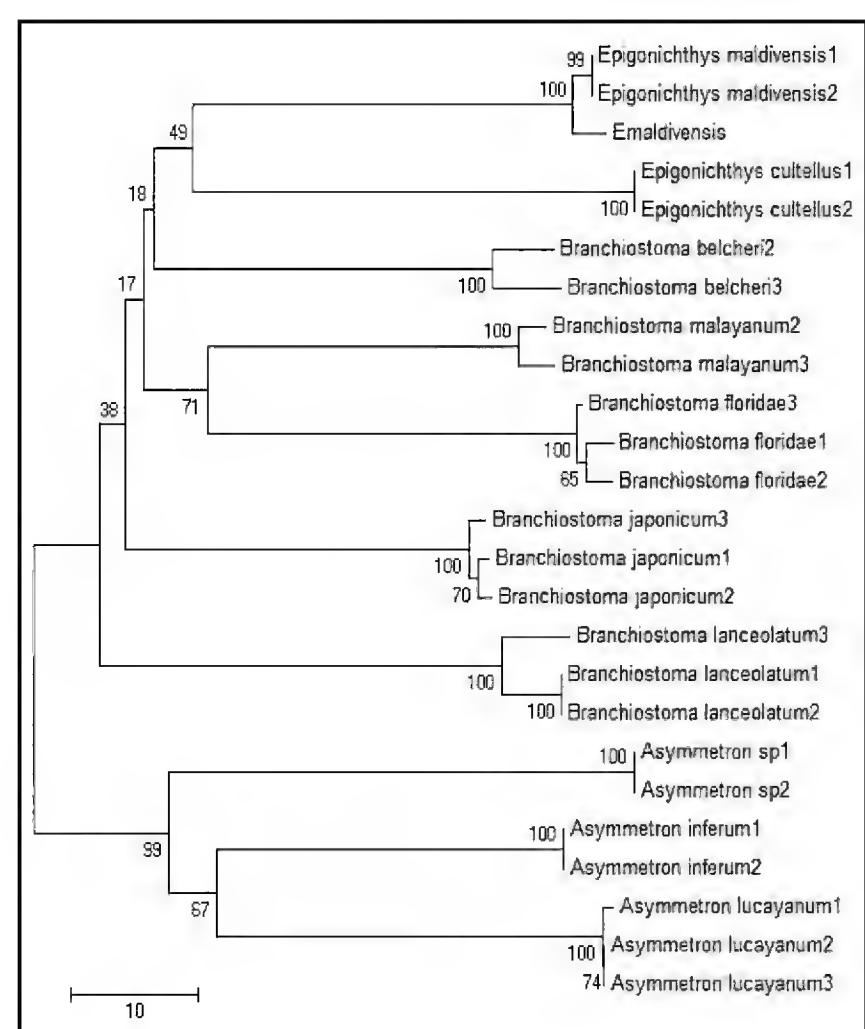


Figure 2. Neighbour-joining tree of the COI sequences for the Branchiostomidae species. The number at the tree nodes indicates the bootstrap values from 10,000 replicates. The figure shows also the GenBank Accession Numbers.

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## Description of three new subspecies of *Carabus* Linnaeus, 1758 (subgenus *Coptolabrus* Solier, 1848) and taxonomic changing on some *Carabus* from Far East of Russia (Coleoptera Carabidae Carabinae)

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### ABSTRACT

Three new *Carabus* Linnaeus, 1758 (subgenus *Coptolabrus* Solier, 1848) subspecies from Far East of Russia and Central China (Anhui Province, Chongqing Province) are described and figured: *C. (Coptolabrus) smaragdinus losevi* n. ssp., *C. (Coptolabrus) elysii wangguofeni* n. ssp. and *C. (Coptolabrus) ignigena tenuitarsatus* n. ssp. Comparative notes with the closest taxa are provided. *Carabus (Morphocarabus) hummeli vladobydovi* Obydov, 2007, *C. (Aulonocarabus) gossarei mareschii* Rapuzzi, 2010, *C. (Megodontus) vietinghoffii rugicolor* Rapuzzi, 2010 and *C. (Coptolabrus) smaragdinus robinzoni* Rapuzzi, 2010 recently considered as synonyms are resurrected as valid subspecies.

### KEY WORDS

*Carabus*; *Coptolabrus*; new subspecies; Far East Russia; China; taxonomic changing.

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## INTRODUCTION

The study of some Coleoptera Carabidae of the genus *Carabus* Linnaeus, 1758 (subgenus *Coptolabrus* Solier, 1848 see Hauser, 1921, 1932a, 1932b; Deuve & Font, 1998; Deuve, 2004) preserved in the author's collection in part provided by Mr. Oleg Losev (Pavlovo, Russia) and Mr. Xi Huangshun (Shanghai, China) gives the opportunity to individuate three new subspecies: *C. (Coptolabrus) smaragdinus losevi* n. ssp. from South Primorye in the Far East of Russia, *C. (Coptolabrus) elysii wangguofeni* n. ssp. from Anhui province, Central China and and *C. (Coptolabrus) ignigena tenuitarsatus* n. ssp. from Chongqing province, Central China.

In the second part of this paper five *Carabus* taxa recently considered as synonyms by Sundukov (2013) are resurrected as valid subspecies.

## RESULTS

### *New taxa*

#### *Carabus (Coptolabrus) smaragdinus losevi* n. ssp.

EXAMINED MATERIAL. Holotype: 1 male, Far East of Russia, South Primorye, Khasanskiy district, Furugelm Island, 11/13.VII.2013, O. Losev legit; preserved in the author's collection. Paratypes: 6 males and 3 females, Far East of Russia, South Primorye, Khasanskiy district, Furugelm Island, 11/13.VII.2013, O. Losev legit; 6 males and 3 females, Far East of Russia, South Primorye, Khasanskiy district, Krabbe peninsula, 30.VI/11.VII.2012, O. Losev legit; 25 males and 3 females, Far East of Russia, South Primorye, Khasanskiy district, Krabbe peninsula, 7/18.VII.2013, O. Losev legit; 24 males and 3 females, Far East of Russia, South-

west Primorskiy region, Khasanskiy district, Mramornyy cape env., 42°34'N; 130°48'E, 28.VII/12.VIII.2012, A. Plutenko legit.

The paratypes are preserved in the author's collection, O. Losev collection and A. Plutenko collection (Russia).

**DESCRIPTION OF HOLOTYPE MALE.** Length including mandibles: 31 mm, maximum width of elytra: 9.8 mm (Fig. 1). Head and pronotum copper-red, elytra copper-red with copper-green sides, relatively shiny; primary and secondary relieved intervals of elytra black. Ventral side of pronotum and epipleura copper-red, metallic, abdomen dark violet; palpi antennae and legs black. Head elongate; surface strongly and uniformly punctured; supra-antennary ridge bent upwards; clypeus relieved, lateral ridges very deep and punctured. Mandibles very long and thin, of "cychrisant" shape. Eyes emispheric and prominent. Labrum bilobate, multi-setulose. Very long and developed palpi, sub-apical segment of labial palpi bi-setose; apical segment of maxillary and labial palpi dilated. Antennae thin, extending with 4 antennomers beyond the base of pronotum and extending more or less the third of elytra. Disc of pronotum nearly flat; sides of pronotum narrow margined, slightly bent upwards at the base; hind angles rounded and very slightly protruding behind its base; surface of pronotum uniformly and very densely punctured, faintly roughly. Elytra quite elongate, oval, very convex, maximum width at the middle; shoulders narrow, slightly pronounced; sculpture triploid heterodyname type: primary intervals forming tubercles of oval shape, smooth; secondary smaller, rounded and very smooth; tertiary completely reduced. Legs very long and strong. Aedeagus: the median lobe in lateral view (Fig. 2) is regularly curved, apex long and curved; dorsal view in figure 3.

**VARIABILITY.** Paratypes have a small variability: the length of the body ranges from 27.5 mm to 32 mm for the males and from 27 mm to 34 mm for the females. The colour of the specimens from Krabbe peninsula is copper green; the specimens from Furugelm island and Mramornyy cape have constantly the holotype colour.

**ETIMOLOGY.** This new interesting *Coptolabrus* subspecies is very cordially dedicated to Mr. Oleg Losev (Pavlovo, Nizhegorodskaya region, Russia) who collected part of the specimens.

**REMARKS.** The small size, the convex shape of elytra with smooth intervals, the quite transverse and of hexagonal shape pronotum, the very small and elongate head and the dominant copper-red colour characterize the new subspecies.

From *C. (Coptolabrus) smaragdinus mandschuricus* Semenov, 1898 the new subspecies is distinguish for the smaller size and for the sculpture of elytra formed by larger and smoother intervals.

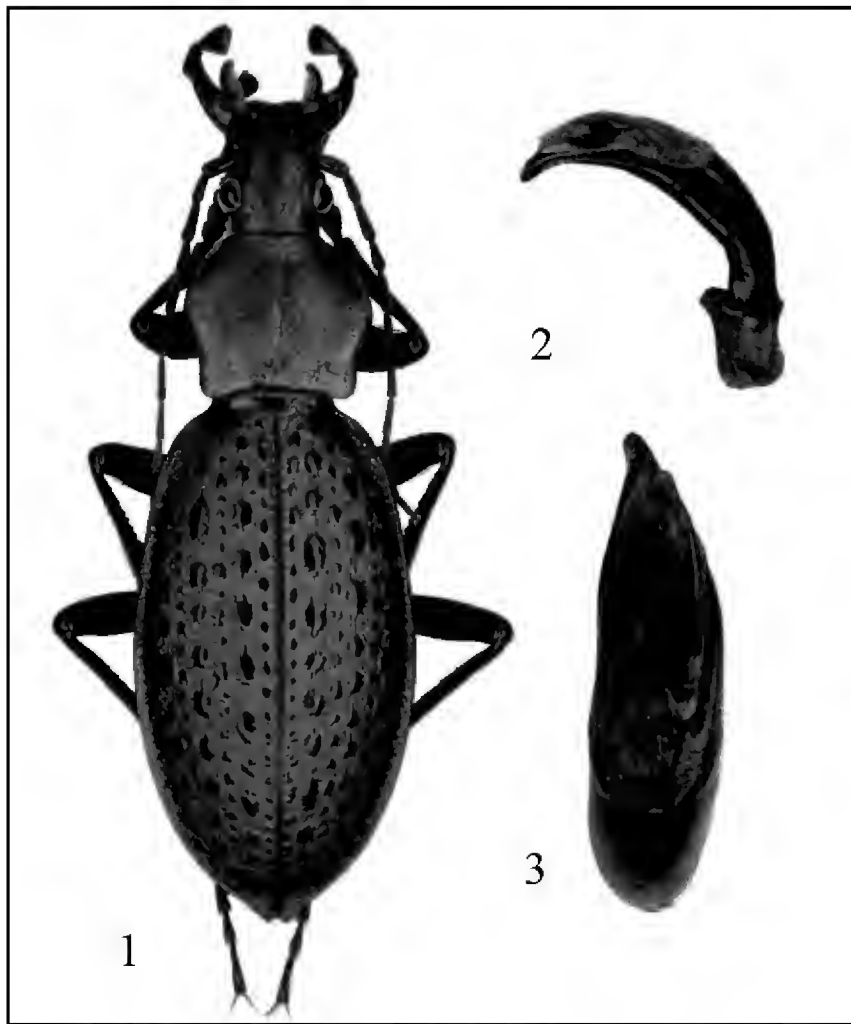
From *C. smaragdinus coreicus* Hauser, 1921 the new subspecies is geographically separate by the large Tumen Jiang river valley and differs for the smaller head, the smaller size, the longer mucrons of elytra, the larger pronotum and smoother sculpture of elytra.

The closest subspecies is *C. smaragdinus robinsoni* Rapuzzi, 2010 described from Reyneke Island near Vladivostok (Rapuzzi, 2010; 2012). With the new subspecies it shares the same small size but differs for the dominant red colour, the transverse pronotum of hexagonal shape, the very convex elytra, the less raised sculpture of elytra and for the shape of aedeagus more curved with longer apex.

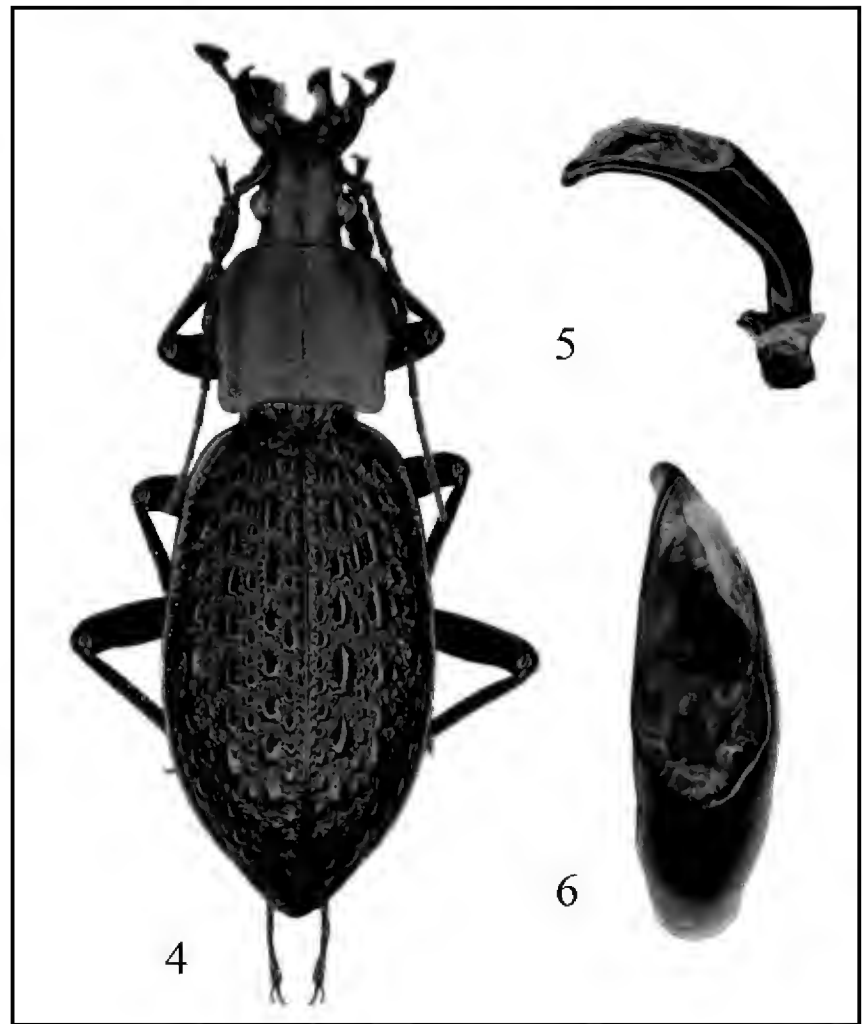
***Carabus (Coptolabrus) elysii wangguofeni* Rapuzzi et Huangshun n. ssp.**

**EXAMINED MATERIAL.** Holotype: male, China, Anhui province, Taihu, Wangling vill., South slope of Mt. Dabieshan, 400 m, 10/30.IV.2015, (30°31'18" N; 116°16'39" E), Xihuangshun legit; preserved in Ivan Rapuzzi collection. Paratypes: 9 males and 11 females, China, Anhui province, Taihu, Wangling vill., North slope of Mt. Dabieshan, 400 m, 10/30.IV.2015, Xihuangshun legit; 3 females, idem, except V.2014; the paratypes are preserved in Ivan Rapuzzi collection.

**DESCRIPTION OF HOLOTYPE MALE.** Length including mandibles: 41 mm, maximum width of elytra: 13 mm (Fig. 4). Upper surface metallic, dull; head green; pronotum and side of elytra gold-green; disc of elytra olive green; primary and secondary intervals of elytra black. Ventral side of pronotum and epipleura green, metallic, abdomen dark violet; appendix black. Head elongate; surface strongly punctured, frons convex and punctured; clypeus very sparsely punctured; clypeus fovea deep and punctured. Mandible long, sickled shape. Palps long with the apical segment strongly dilated;



Figures 1–3. *Carabus* (*Coptolabrus*) *smaragdinus losevi* n. ssp. holotype male. Fig. 1: holotype. Fig. 2: holotype male aedeagus: median lobe in lateral view. Fig. 3: idem, apex in dorsal view.



Figures 4–6. *Carabus* (*Coptolabrus*) *elysii wangguofeni* n. ssp. holotype male. Fig. 4: holotype. Fig. 5: holotype male aedeagus: median lobe in lateral view. Fig. 6: idem, apex in dorsal view.

penultimate segment of labial palps bi-setose. Pronotum of hexagonal shape, transverse (1.21 times as long as broad); base of pronotum large; sides quite rounded, marginated, bent upwards; basal lobes large and rounded, protruding its base; surface of pronotum densely and shallow punctured. Elytra oval; disc convex; mucrones short; sculpture triploid heterodyname type: primary tubercles rounded and close; secondary smaller and rounded; tertiary forming grains strongly rough; ground roughly sculptured. Legs quite short. Male aedeagus (Figs. 5, 6).

**VARIABILITY.** Very variable in colour: green, bluish-green, blue, golden-green; the margins often differ from the discs of pronotum and elytra; colour of head and pronotum often contrasting with that of elytra. The colour always has cold tints. The length of the body ranges from 37 mm to 41 mm for the males and from 40 mm to 44 mm for the females. One female specimens has the sculpture of elytra with tubercles more elongate.

**ETIMOLOGY.** The beautiful new *Coptolabrus* taxa is very cordially dedicated to Mrs. Wang Guo-

fen (Shanghai, China) wife of Mr. Xi Huangshun. The co-author of this new subspecies is Huangshun Xi from Shanghai, China

**REMARKS.** From Southern Anhui several *Coptolabrus* taxa are known:

*Carabus* (*Coptolabrus*) *elysii elysii* Thomson, 1846: Ngang-Wei, Anking (= Anhui, Anqing) (Hauser, 1921);

*Carabus* (*Coptolabrus*) *elysii connectens* Hauser, 1912: Ngang-Wei, südlicher Teil (= Anhui, Southern part) (Hauser, 1921);

*Carabus* (*Coptolabrus*) *elysii anhweiensis* Hauser, 1932: Anking (= Anqing) (Hauser, 1932a loc. typ.; 1932b). Very close to *C. elysii connectens* it is considered as a synonym by Brezina (2003);

*Carabus* (*Coptolabrus*) *lafossei tungchengensis* Li, 1993: Tongcheng Xian, Longming, Shanling, locus typicus (Li, 1993);

*Carabus* (*Coptolabrus*) *lafossei dabieshanus* Imura, 1996: Anhui: Dabie Shan, Yuexi, Mt. Miaodaoshan, locus typicus (Imura, 1996); Hetupu (Deuve, 1997); Qianshan Xian, Tianzhu Mt. (Imura, 1996); Qian Shan; Jiuhua Shan; Baima Jian



(Kleinfeld, 1997). Very close to *C. (Coptolabrus) lafossei tungchengensis* it is considered as a synonym by Brezina (2003)

*Carabus (Coptolabrus) lafossei jingdensis* Deuve et Li, 2006: Anhui, Jingde Xian, Junle, 30°20'N; 118°30'E, locus typicus (Deuve et Li, 2006).

From the adjacent area were described:

*Carabus (Coptolabrus) lafossei tiantai* Kleinfeld, 1997: NE-Hubei: Hong'an, Mt. Tiantai, 31:23N/114:37E, locus typicus (Kleinfeld, 1997);

*Carabus (Coptolabrus) lafossei pseudocoelestis* Kleinfeld, 1999: N-Hubei, Shuizhou, Dahong Mt., 31:29N/112:58E, 1200 m, locus typicus (Kleinfeld, 1999);

*Carabus (Coptolabrus) elysii pulcher* Kleinfeld, 1997: S-Henan, S of Xinyang, Jigong Shan, 31:49N/114:06E, locus typicus (Kleinfeld, 1997).

The closest form is *C. elysii pulcher* from which the new subspecies is easily distinguished by the following characters: smaller size, very different colour with domination of cold tints; larger pronotum with smoother sides (less angulate); more convex elytra; shorter elytral mucrones; primary intervals forming smaller and nearly perfect rounded tubercles.

From *C. elysii elysii* and *C. elysii anhweiensis* the new subspecies differs by: larger size; more elongate and slender body shape; hexagonal pronotum; rounded and raised primary tubercles (smoother in *C. elysii elysii* and *C. elysii anhweiensis*); longer elytral mucrones.

The range of the new subspecies is geographically very close to that of *C. lafossei dabiesanus* but very easily distinguishable by several strong characters: different colour (in *C. lafossei dabiesanus* constantly with black elytra and dark blue elytra margins, head and pronotum); more transverse and less angulate pronotum; upper surface of head and pronotum strongly punctured (smooth in *C. lafossei lafossei*); different sculpture of elytra and shorter mucrons of elytra.

From *C. lafossei tiantai*, *C. lafossei pseudocoelestis* and *C. lafossei jingdensis* the new taxon has all the distinctive characters of the species that permit to separate *C. elysii elysii* from *C. lafossei lafossei*. *Carabus lafossei tiantai* and the new subspecies show, in part, the same colour.

***Carabus (Coptolabrus) ignigena tenuitarsatus***  
n. ssp.

EXAMINED MATERIAL. Holotype: male, China, Chongqing province, Pengshui county, Mt. Heimending, local collector legit; preserved in the author's collection. Paratype: 1 male, China, Chongqing province, Pengshui county, Mt. Heimending, local collector legit; the paratype is preserved in the author's collection.

DESCRIPTION OF HOLOTYPE MALE. Small size and very thin shape for the species, length including mandibles 38.5 mm; maximum width of elytra 11.8 mm (Fig. 7). Upper surface metallic, rather mat; head with supra antennary ridges green; pronotum with sides gold green, disk darker; elytra uniformly green, sides very shine, brilliant; primary and secondary intervals black. Ventral face of head black; ventral face of pronotum and epipleura dark green, metallic; abdomen black with violet shades, metallic; appendix black. Head long and very slender; surface of head densely punctured, frons very convex. Mandibles elongate. Eyes quite small and slightly salient. Palpi long with the apical segment strongly dilated; penultimate segment of labial palpi bisetose. Pronotum long and very narrow for the species, as broad as long. sides of pronotum very sinuate, rounded; hind angles salient and very few protruding behind the base; upper surface flat; surface of pronotum densely punctured, median sulcus very superficial. Elytra narrow and very elongate for the species, ovals; disc convex. Primary intervals perfectly rounded or slightly elongate, very prominent; secondary forming aligned grains; tertiary reduced. Long mucrones. Legs quite short. First and second protarsal segments of male slightly dilated with complete adhesive soles; the third male protarsal segment not dilated and with very rudimental adhesive soles.

Male aedeagus (Figs. 8, 9) is characteristic for the species but quite slender and of narrower shape.

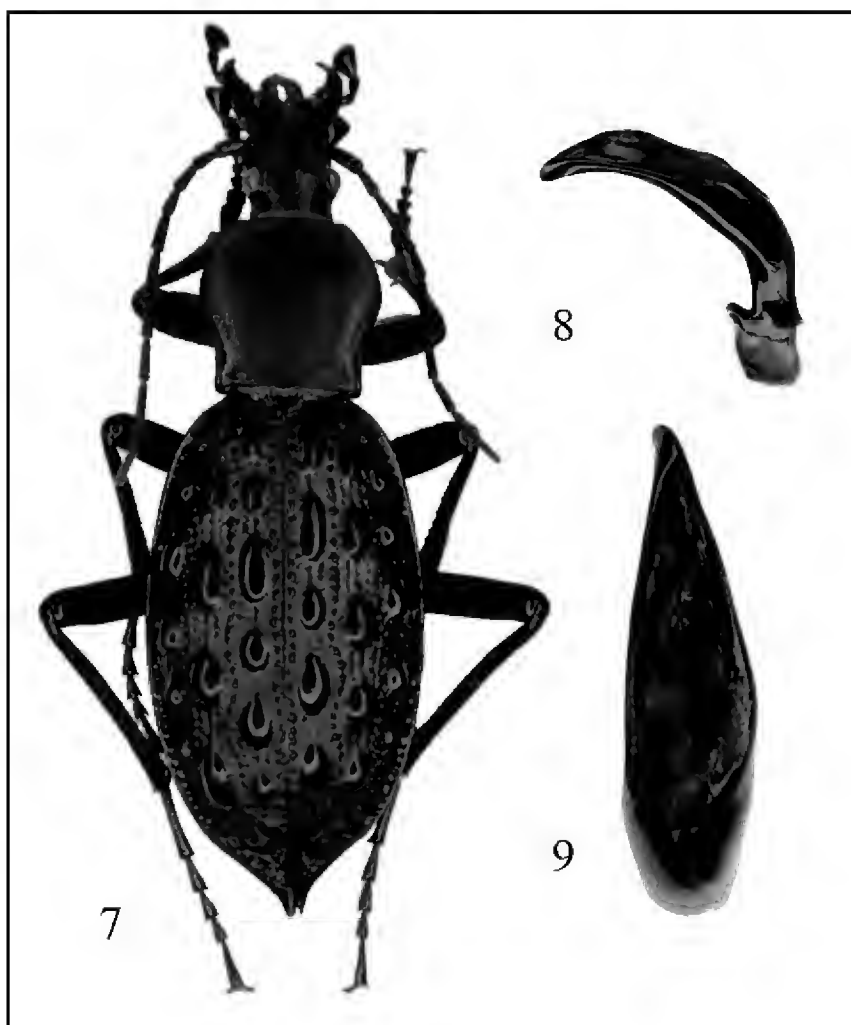
VARIABILITY. No significant variability of the paratypes

ETIMOLOGY. The new subspecies is named after the slightly dilated male protarsal segments.



REMARKS. As expected the new taxa is morphologically close to the northern most subspecies of *C. ignigena*: *C. (Coptolabrus) ignigena cristianofonti* Deuve et Font, 2008 and *C. (Coptolabrus) ignigena tongrenensis* Deuve et Li, 2006.

From *C. (C.) ignigena cristianofonti*, that it is the closest form, it is easily distinguished by the following characters: slender shape of head and pronotum; sides of pronotum sinuate but not angled; much elongate elytra with primary intervals more relieved; protarsal segments of male slightly dilated, the third segment not dilated and with very rudimental adhesive soles. From *C. (C.) ignigena tongrenensis* the new subspecies is distinguished by the following characters: smaller size; slender shape of head and pronotum; primary intervals of elytral sculpture more prominent; shorter legs; protarsal segments of male slightly dilated, the third segment not dilated and with very rudimental adhesive soles. Up to now the new subspecies is the northernmost population of the whole range of *C. ignigena* and it is the first record of the species for the Chongqing province.



Figures 7–9. *Carabus (Coptolabrus) ignigena tenuitarsatus* n. ssp. holotype male. Fig. 7: holotype. Fig. 8: holotype male aedeagus: median lobe in lateral view. Fig. 9: idem, apex in dorsal view.

### Taxonomic notes

Recently Sundukov (2013) established as synonyms four *Carabus* subspecies described from the Peter the Great Gulf Islands, Vladivostok area, Far East of Russia: *C. (Morphocarabus) hummeli smaragdulus* Kraatz, 1878 = *C. (M.) hummeli vladobydovi* Obydov, 2007); *Carabus (Aulonocarabus) gossarei gossarei* Haury, 1879 = *C. (A.) gossarei mareschii* Rapuzzi, 2010; *Carabus (Megodontus) vietinghoffi bowringi* Chaudoir, 1863 = *C. (M.) vietinghoffi rugicolor* Rapuzzi, 2010 and *C. (Coptolabrus) smaragdinus mandschuricus* Semenov, 1898 = *C. (C.) smaragdinus robinzoni* Rapuzzi, 2010. For the significant morphological characters and the perfect isolation under insular conditions all these taxa will be resurrect:

- *Carabus (Morphocarabus) hummeli vladobydovi* Obydov, 2007 stat. resurr. Described from Popov Island (Obydov, 2007) *C. hummeli vladobydovi* has good morphological characters that permit to separate it from the populations from the mainland as well as from *C. hummeli putyatini* Rapuzzi (2012) from Putyatin island. *Carabus hummeli vladobydovi* differs from all the other known *hummeli* subspecies for its very peculiar coloration: violet-pink or red-pink pronotum, pink with gold or green shades elytra and purple margins.

- *Carabus (Aulonocarabus) gossarei mareschii* Rapuzzi, 2010 stat. resurr. Described and known only from the Askol'd Island *C. gossarei mareschii* is easily separable from *C. gossarei gossarei* by several characters: larger size and more developed elytra of ovate-elongate shape. The pronotum is less punctate with larger and deeper basal impressions. Elytral sculpture with less interrupted and less prominent primary intervals. Male aedeagus longer and larger with the median lobe more developed.

- *Carabus (Megodontus) vietinghoffii rugicolor* Rapuzzi, 2010 stat. resurr. Described from Reyneke Island it is one of the most distinctive subspecies of *C. vietinghoffii*. It is easily distinguished from *C. vietinghoffii bowringi* by significant and constant characters: in general bigger and stronger shape; very different colour: upper surface dark red to black-violet, rather mat, margins of elytra of the same colour. Male aedeagus differs for: in lateral view the median lobe is more developed and the apical lobe is longer; apex in frontal view curved on the left.

- *Carabus (Coptolabrus) smaragdinus robinzoni* Rapuzzi, 2010 stat. resurr. Described from Reyneke Island it differs from *C. smaragdinus mandschuricus* by the following characters: smaller size; slender and flatter shape; pronotum as broad as long, not transverse; stronger elytral sculpture; apical lobe of male aedeagus longer and slender. It is interesting to note that *C. smaragdinus robinzoni* is very constant in his type locality.

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# On the presence of the Andaman lobster, *Metanephrops andamanicus* (Wood-Mason, 1891) (Crustacea Astacidea Nephropidae) in Palabuhanratu bay (S-Java, Indonesia)

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## ABSTRACT

The first Andaman lobster, *Metanephrops andamanicus* (Wood-Mason, 1891) (Crustacea Astacidea Nephropidae) record from south of Java waters, part of Indian Ocean is reported in this paper. A total of 3 specimens were collected at a fish harbor in Palabuhanratu bay in May 2015. Morphological characters are illustrated and described. This finding enhances the biodiversity lists of Indonesian crustaceans.

## KEY WORDS

Andaman lobster; Decapoda; Indian Ocean; Java Island; morphological descriptions.

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## INTRODUCTION

The lobsters of the family Nephropidae are deep-sea forms and commonly found at depths from 150 to more than 1893 m (Chang et al., 2014). In general nephropid lobsters are bottom-dwellers with a preference for soft sediments, and living within their self-made burrows is the biological behavior in some species (Chan, 1998).

The family Nephropidae currently includes 57 species belonging to 14 genera (Holthuis, 1991; Chan, 1998; Türkay, 2001; Chan, 2010; Ahyong et al., 2012; Chan et al., 2014). Previously, genus *Metanephrops* Jenkins, 1972 was divided into four morphological groups, namely *thomsoni* (Bate, 1888), *binghami* (Boone, 1927), *arafurensis* (De Man, 1905) and *japonicus* (Tapparone-Canefri, 1873) (Holthuis, 1991). However, with molecular analysis approach, Chan et al. (2009) refuted monophyly of the *arafurensis* and *thomsoni* groups.

Among the groups, *japonicus* has the highest number of species.

Some of the current researches on Indonesian crustaceans, reported the presence of first records species, especially hippoid crabs, such as *Albunea symmysta* (Linnaeus, 1758) (Mashar et al., 2015), *Hippa marmorata* Hombron et Jacquinot, 1846) (Wardiatno et al., 2015), *Hippa adactyla* Fabricius, 1787 (Ardika et al., 2015).

This paper presents a new record of the Andaman lobster, *Metanephrops andamanicus* (Wood-Mason, 1891) from south of Java, Indonesia.

## MATERIAL AND METHODS

Three *M. andamanicus* specimens were collected in May 2015, from a fish harbor in Palabuhanratu bay, District Sukabumi, South of Java, Indonesia (Fig. 1). They were preserved in 96%

alcohol and taken to the laboratory for analysis. Identification was based on the morphological characters using taxonomic key books from FAO (Holthuis, 1991; Chan, 1998). One example of the specimens is presented in figure 2. The specimens were lodged in the Department of Aquatic Resources Management, Bogor Agricultural University, Indonesia.

## RESULTS

### SYSTEMATICS

Infraorder ASTACIDEA Scholts et Richter, 1995

Family NEPHROPIDAE Dana, 1852

Genus *Metanephrops* Jenkins, 1972

*Metanephrops andamanicus* (Wood-Mason, 1891)

EXAMINED MATERIAL. 3 males: carapace length 51.04, 55.97, and 57.20 mm, total length 141.82, 149.34, and 154.23 mm, weight 65, 78, and 88 gram. 17.V.2015, Palabuhanratu fishing harbor, South of Java, Indonesia.

DIAGNOSIS. Carapace of *M. andamanicus* smooth between ridges and large spines (Fig. 3). Eyes large and black, postrostral carinae with three teeth (Fig. 4). Surface of abdominal tergites conspicuously sculptured; raised parts of dorsal surface of abdominal somites smooth and naked; second to fifth abdominal somites with marked dorsomedian carina, flanked by pair of conspicuous longitudinal grooves (Fig. 5). Fifth abdominal somite without distinct spines on carina separating tergite from pleuron. Dorsomedian carina of sixth abdominal somite without submedian spines. Spine in middle of lateral margin of sixth abdominal somite short, tip far from posterolateral margin of somite. Chelae of first pereopods heavily ridged and spinulose, without large spines; no prominent basal spine on outer edge of movable finger of large chela. Inner margin of merus of first pereopod weakly spinulose (Fig. 6).

DISTRIBUTION. Indo-West Pacific region: East Africa (Tanzania, Zanzibar, Kenya and Somalia), the Andaman Sea, the South China Sea (not including the Philippines), and Indonesia, and perhaps also Papua New Guinea (Holthuis, 1991; Chan, 1998; Tshudy et al., 2007).

## DISCUSSION

Holthuis (1991), Chan (1998) and Tshudy et al. (2007) revealed the distribution of *M. andamanicus* in Indo-West Pacific region from eastern Africa to the Andaman Sea, the South China Sea (but not the Philippines), Indonesia, and perhaps also Papua New Guinea. According to the IUCN Red List of Threatened Species the occurrence of the species in Indonesia was reported in Kalimantan, Sumatra and Sulawesi. However, in a short survey on May 2015 we could find this species in Palabuhanratu bay located in south of Java and it is a new record. Some lobster species were previously reported from several parts of Indonesia, and they were highly valuable species, such as *Panulirus penicillatus* (Olivier, 1791) (Chow et al., 2011; Kalih, 2012; Abdullah et al., 2014), *Linuparus somniosus* Berry et George, 1972 (Wowor, 1999), *P. versicolor* (Latreille, 1804) (Ongkers et al., 2014), *P. homarus*, (Linnaeus, 1758), *P. longipes* (A. Milne-Edwards, 1868), *P. ornatus* (Fabricius, 1798), *Parribacus antarcticus* (Lund, 1793) (Kalih, 2012). Consequently, the presence of *M. andamanicus* in Palabuhanratu bay increases the list of lobster biodiversity in Indonesian waters.

In fishery point of view, some species of genus *Metanephrops* have commercial potential and become the deep water fishery targets lobster and caught by trawl; those species are *M. mozambicus* (Macpherson, 1990) in Africa (Fennessy & Groeneveld, 1997; Groeneveld & Everett, 2015), *M. thomsoni* in northern part of the East China Sea (Choi et al., 2008), *M. challengerii* (Balls, 1914) in New Zeland (Tuck et al., 2015), *M. andamanicus* in east coast of Southern Africa (Mutagyera, 1979). In the fish market located in Palabuhanratu bay, south of Java *M. andamanicus* can be regularly found indicating its economical value in the area.

As fishery target, biological information of this species is needed for its sustainable management. Exploration in biological aspects of *M. andamanicus* is open for future studies.

## ACKNOWLEDGEMENTS

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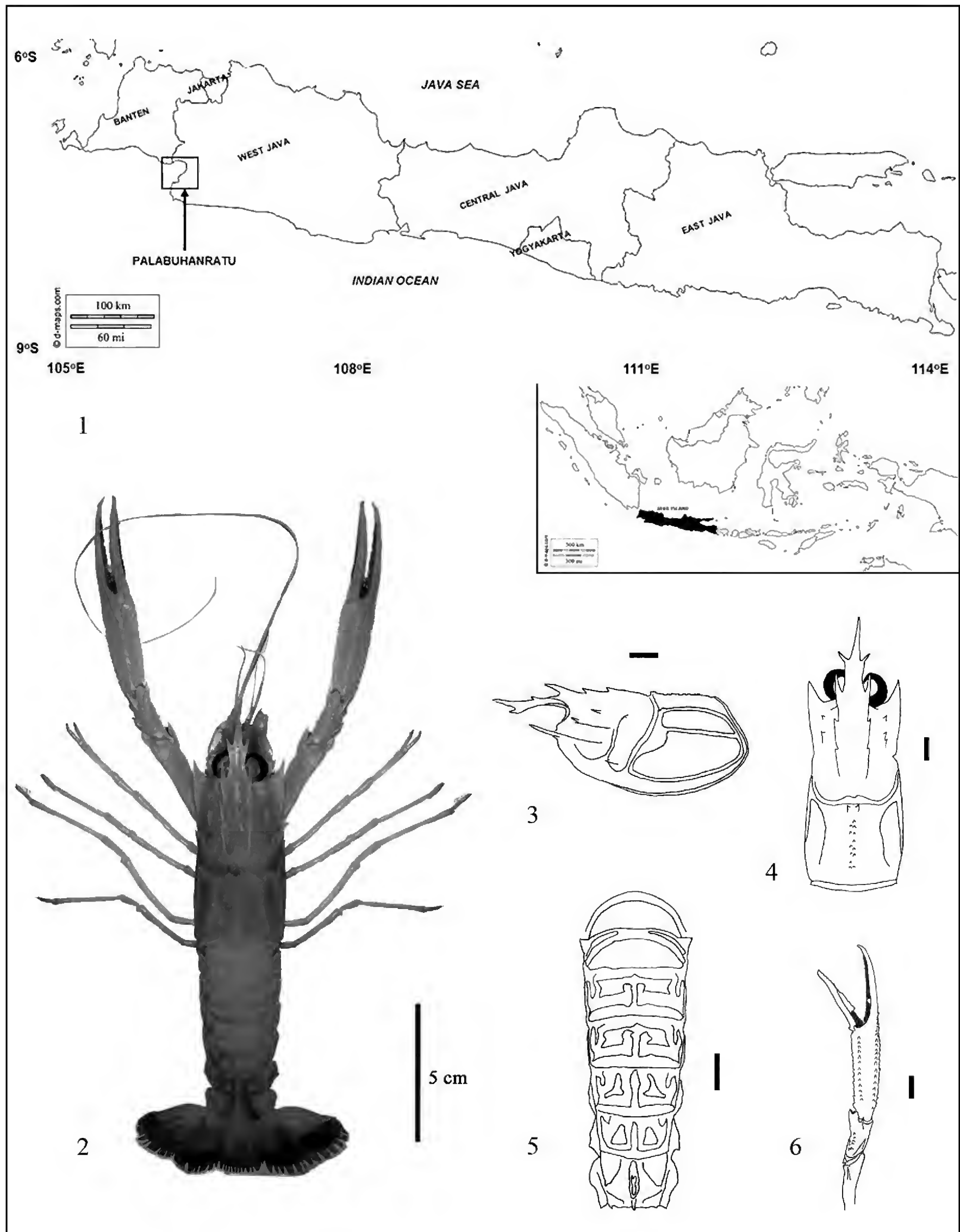


Figure 1. Map of Java Island with the insert map of Indonesia. Palabuhanratu bay is indicated by open-square and pointed with an arrow. Figure 2. *Metanephrops andamanicus* (male) collected from a fish harbor in Palabuhanratu Bay, south of Java, Indonesia. Figures 3–6. *Metanephrops andamanicus*, south of Java (Indian Ocean), male (carapace length 55.97 mm). Fig. 3: carapace, lateral view. Fig. 4: carapace, dorsal view. Fig. 5: abdomen, dorsal view. Fig. 6: first pereopod. Scale bars 10 mm.



Fiscal Year 2015. The authors wish to thank to Mr. Agus for his assistance during specimen collection.

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## Does local knowledge change after a species long term absence? The case of giant river otters *Pteronura brasiliensis* Gmelin, 1788 (Carnivora Mustelidae)

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### ABSTRACT

Public participation could be useful to determine species presence and ecological aspects, however it is possible that local knowledge of species whose populations had suffered a decrease could have changed. To determine current knowledge of giant river otter, *Pteronura brasiliensis* Gmelin, 1788 (Carnivora Mustelidae), we undertook a preliminary assessment based on 35 interviews performed between June and August 2014 with natural resources users in the Pacaya-Samiria Reserve (Peru) aimed to determine the presence, feeding habits, reproduction periods, and threats. It was possible to determine that current knowledge correspond with available information in literature thus, I consider that it is possible to use public participation in cases of little known species that are recovering.

### KEY WORDS

Public monitoring; *Pteronura*; Pacaya-Samiria Reserve; endangered species.

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Habitat loss, fragmentation, and degradation, along with other human-related causes have put most ecosystems and the species that inhabit them at risk (Myers, 1988). Therefore, conservation strategies rely on the prioritization of areas that are key for the long term survival of many species. Such prioritization becomes more important in areas with high biodiversity; and even more so when these areas are related with high human densities, where actions are needed sooner rather than later (Sanderson et al., 2002). However, information on both ecosystems and species at regional level is often missing making it necessary to generate a strategy that could help to increase knowledge at this level. It has been proposed that this kind of information can be obtained from the general public as a first step for management; as scientific research

is usually limited in space and time (i.e. short term studies in a specific site) making some changes to go either unperceived or identified after a huge gap of time (Scholte, 2011). Just to mention, in Madagascar local knowledge has been used to shape distribution of carnivore species (Kotschwar et al., 2015) and in Zimbabwe to determine population trends of different carnivore and game species (Gandiwa, 2012).

However, there is not enough information on how local knowledge and perception changes after a charismatic species disappears from a region such as in the case of the giant river otter, *Pteronura brasiliensis* Gmelin, 1788 (Carnivora Mustelidae). This species was once distributed in most freshwater streams of South America, from Venezuela to Argentina (Eisenberg, 1989). Its numbers have

decreased significantly up to the extent that some populations have disappeared from its former range due hunting and habitat loss (Carter & Rosas, 1997; Recharte & Bodmer, 2010). The species is currently listed as endangered by the red list (IUCN, 2016) with a projected population decrease of about 50% within the next twenty years (Shostell & Ruiz-Garcia, 2013). Fortunately, due a ban on hunting and a decrease on its commercial demand in Peru, giant river otter populations have increased in certain areas such as in the Yavarí River (Recharte & Bodmer, 2010) and in the Pacaya-Samiria National Reserve in Perú (Groenendijk et al., 2001). The species is important at local level as it is considered a top predator and due its potential as a bio indicator as it is especially sensitive to disturbance and resource availability, preferring conserved areas with good fish stocks (Carter & Rosas, 1997; Groenendijk et al., 2001; Recharte & Bodmer, 2010). Unfortunately, scientific information of the species along its range is scarce except for a few areas (e.g. Madre de Dios: Hajek & Groenendijk, 2006) and Pacaya-Samiria National Reserve (Groenendijk et al., 2001). However, there is not enough information on how local knowledge and perception changed after the long term absence of the species in the region. Thus, it is important to determine if users of natural resources are aware of the giant

river otter presence and ecology in order to include their knowledge in management plans.

I undertook semi structured interviews with the natural resource users of the Pacaya-Samiria National Reserve in northeastern Peru to assess their actual knowledge on giant river otters (Fig. 1). The Pacaya-Samiria National Reserve is located in the Amazon Basin and is considered the largest protected area of flooded forest in the Amazon with 20,800 km<sup>2</sup> (Bodmer et al., 2011). Its average annual rainfall is 2000–3000 mm and a mean temperature between 20 and 33°C (Bodmer et al., 2011). The reserve and its buffer zone have 203 rural settlements; most of them (89%) are small villages with less than 500 inhabitants located on the borders of the Marañón and Ucayali/Puinahua rivers (González, 2003). The households in the area include people of mixed origins (mestizos), natives from the ethnic groups Cocama-Cocamilla and Shipibo-Conibo, whose major economic activities include fishing, agriculture, game hunting, and extraction of forest products (González, 2003). Some communities have been actively involved in groups of natural resources management in the Reserve (Puertas et al., 2000; Piana et al., 2003). I concentrated my efforts in the Samiria River, a black water river preferred by giant river otters (Carter & Rosas, 1997). I used the vigilance point 2 known as “Tacshacocha” as interviewing place, since visitors and members of the community management groups have to register when travelling upriver.

I made a total of 35 interviews between June and August 2014. The survey consisted in a set of 22 questions aimed to determine the presence of the species, habitat preferences, reproduction patterns and potential threats to giant river otters. Interviewed persons belong to five different communities: Leoncio Pradro (47%), San Martín de Tipishca (29%), San Carlos (12%), Santa Rita (3%) and Victoria (9%). On average, the interviewees were 41 years old. Half of them (50%) belong to one of the local community-based conservation groups which were formed aiming for the sustainable use of natural resources as well as turtle management and conservation; they also serve as guides for scientific groups (19%). Sixty-nine percent of the interviewees typically use the reserve throughout the year, another 22% use it only during the dry season. Therefore, I considered that responses were based on field experience.

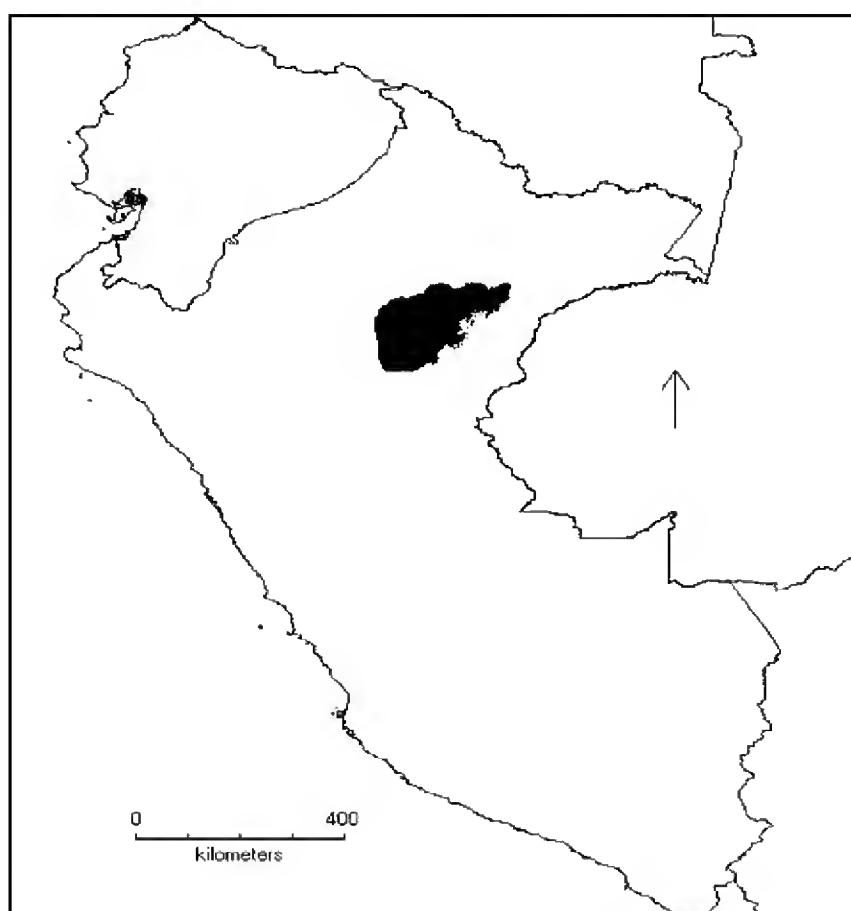


Figure 1. Pacaya-Samiria National Reserve in Northeastern Peru.

Locals stated that otters can be observed throughout the year (40% of interviewees), but that are easier to detect during the dry season (43%). These observations can be explained because their movements are concentrated to lakes and rivers during the dry season, while they move to flooded forests and small creeks during the wet season (Hajek & Groenendijk, 2006), becoming scattered and harder to detect. Moreover, 53% of the respondents identified both river and rainforest as preferred habitats and another 41% considered river as the main one. Locals also reported diurnal observations (54% of interviewees), especially during the early hours of the morning (34%). This is supported by Carter & Rosas (1997), who identified giant river otters as diurnal. Interviewees reported that the main activities conducted by the river otters were playing, feeding, fishing, and vigilance, which correspond with previous reports about their daily activity (Carter & Rosas, 1997; Hajek & Groenendijk, 2006).

The diet of the giant river otter varies with habitat type and species diversity in the area (Hajek & Groenendijk, 2006). Fish are the main diet component (Carter & Rosas, 1997; Hajek & Groenendijk, 2006), but other groups such as mammals and crabs have also been recorded (Hajek & Groenendijk, 2006). Preferred fish consumed by the giant river otter belong to the suborders Characoidei (characins), Percoidei (perch) and Siluroidei (catfish) (Carter & Rosas, 1997). Accordingly, interviewees identified fish of different species such as carachama (*Pseudorinelepis* spp.) and different types of piranha (Characoidei) as the main diet component of the species.

Knowledge about reproduction and cub development tended to vary. All interviewees considered that otters reproduce in the Samiria River, but only 80% have seen cubs. Eighty-eight percent of locals reported that otters breed during the dry season (May-September), which corresponds with observations in other areas (Duplaix, 1980; Hajek & Groenendijk, 2006). Although litter size is known to vary between one and five cubs per season (Carter & Rosas, 1997; Hajek & Groenendijk, 2006), locals have little knowledge about this fact as just 29% consider that the species had just one cub per year. It is noteworthy that interviewees claimed they cannot differentiate pregnant from non-pregnant females (62%); but they can differentiate adults and cubs by size (76%).

The success on conservation measures that have resulted in river otter population increase (Recharte & Bodmer, 2010) has been noted by interviewees, where 91% considered that the otter population was growing. Otter population increases may lead to a raise in human-otter conflicts. In fact, 49% of them considered the species as harmful to fishing nets and fish stocks, 46% stated that locals are afraid of the giant river otter, and 21% reported known previous attacks to humans. This corresponds with observations made by Carter & Rosas (1997), where people in recently colonized areas of the Amazon forest feared giant river otters. Interviewees suggest fears result from lack of knowledge about the species. Regardless, 91% of the interviewees claimed local communities know that the giant otter is protected. Also, 91% of the respondents considered the giant otter as an important and emblematic species in the area because it represents the reserve and is part of the ecosystem. This is supported by the fact that 92% of them reported that this species is no longer hunted in the area as it is extremely prohibited, except occasionally when cubs are captured to be kept as pets or to be sold to zoos, as previously reported (Duplaix, 1980; Carter & Rosas, 1997).

Our results indicate that, despite the species is still at low densities and was carried almost to the point of local extinction, local people who visit this reserve are well informed about the presence, ecology and distribution of the species. The latter can be confirmed by comparing published information from zoos and field observations about the species with local knowledge. In the specific case of the giant river otter, results showed that it is possible to use local knowledge as baseline information to generate conservation projects and community projects. Thus, it can be considered that for regions with limited information about species and ecosystems it is possible to use public participation, especially of community conservation groups, where available, in order to generate management plans or even monitoring programs.

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# Patterns of Butterfly distribution in Alabama, USA (Lepidoptera)

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## ABSTRACT

Butterflies (Lepidoptera) are an iconic group of insects and are emphasized in ecological research and biodiversity conservation due to the role in ecological processes. Alabama (USA) has 139 species of butterflies in 6 families based on the previous field surveys. In this study the information from the previous field survey was analyzed with environmental information for the general patterns across 67 counties of Alabama. The results indicate that the counties with the higher butterfly species are mainly within the metropolitan areas; power-law relationship exists between average species number and occupied county number; there is higher number of butterfly species at counties with either the highest or the lowest forest coverage; there is positive correlation between latitude and butterfly species density; counties with the lowest or the highest species number usually have higher standard deviations in annual air temperature or precipitation; butterflies with a big distribution area do not have significantly bigger wing size in comparison to ones with a small distribution area; and with the increase of latitude, the average wing size of butterflies increases. The results provide new understanding for the butterfly distribution at a regional level.

## KEY WORDS

Alabama; butterflies; climate; latitude; species number; wing size.

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## INTRODUCTION

The Butterflies (Lepidoptera) play an important role in ecosystems and conduct ecological services (Tiple et al., 2006), such as pollination and herbivores. Butterflies are considered as good ecological indicators of the health of some terrestrial ecosystems (New, 1991; Thomas, 2005; Bonebrake et al., 2010). The beautiful color of butterflies and unique features also provide recreation resource to human society. Butterflies are greater sensitive than other taxonomic groups to reflect human disturbance (Thomas, 2005). Monitoring butterfly species at an area can indicate human mismanagement and pollution (Wilson, 1997). Due to climate change,

altered land use (e.g., habitat loss), and pollutants (e.g., pesticides and herbicides), the butterflies are in declining, such as in Europe (van Swaay et al., 2006). The loss of native plants, which are food for leaf-eating caterpillars and nectar sipping adult butterflies, by the replacement of exotic invasive species has devastated butterflies. Butterflies are an iconic group of insects and are emphasized in ecology and biodiversity conservation.

The state of Alabama (USA) has 139 species of butterflies in six families (Hesperiidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae, and Nymphalidae). The information of distribution, habitat, food, life history and wingspan for all 139 species is listed in the book “Butterflies of Alabama” based on the

field records (Howell & Charny, 2010). This information provides an opportunity for integrated study, such as analyzing patterns of butterfly distribution and uncovering the related factors.

One of the important features of butterflies is their wingspan or body size. Body size is a key trait related to the life history of individuals, the wing size (a proxy for body size) of butterflies significantly decreased in response to warmer summers in high arctic area (Bowden et al., 2015). Based on the Bergmann's rule, larger individuals occur at higher latitudes and in colder environments (Sand et al., 1995). Similarly, smaller adult size should be in higher temperatures or southern area. Although both Bergmann's rule and the temperature-size rule predict larger individuals in colder environments, however, the opposite pattern also reported (Blankenhorn & Demont, 2004; Angilletta, 2009). Several ways were proposed that temperature may affect body size.

Two mechanisms related to external temperatures may impact body size in different directions.

First, the metabolic rates increase with warmer temperatures, organisms become smaller if they cannot offset energy losses under high metabolic costs.

Second, rising temperatures in seasonal environment make longer growing seasons, which may let organisms grow larger.

The extended seasons could also low plant-food quality during late season (Awmack & Leather, 2002). Baguette & Stevens (2013) suggested that wingsize of butterflies is positively related to minimum area requirements. Butterflies with big wing size should have a big distribution area. Host-range relationship may be primarily determined by ecological and population-genetic factors (Barrett & Heil, 2012). For example, generalists should be promoted by volatile host communities, while specialists should be favored in places where host communities are stable (Jaenike, 1990). This means that harsh and volatile climate in a temperate region could have more generalists and favorable and static climate have more specialists. For the distribution area, plants are food and habitats to butterflies, forests harbor between 50% and 90% of Earth's terrestrial species including diverse of plant species (World Resources Institute et al., 1992), there should have more butterfly species in forest areas than at less or none forest areas.

It is also known that butterflies are sensitive to habitat fragmentation (Öckinger et al., 2010), so with the increased landscape fragmentation in one region, such as in a metropolitan area, butterfly species number may decrease. Therefore, the goal of this study is to use the collected butterfly information from Howell & Charny (2010) combined with climate and environmental information to indicate the general patterns of butterfly distribution in the state of Alabama and test the above hypotheses. The specific objectives include (i) distribution pattern of butterfly species along latitude; (ii) relationship between wing size of butterflies and latitude; (iii) relationship between butterfly species number and plant species number and forest cover at county level; and (iv) relationship between butterfly species number and urbanization at the county level. This study will provide understanding of the patterns of butterfly distribution in Alabama.

## MATERIAL AND METHODS

### *Study area*

Alabama is located in the southern region of USA. and between the southern foothills of the Appalachian Mountain Range and the Gulf of Mexico. There are total 67 counties in Alabama (Fig. 1). Since the State of Alabama runs roughly from 31° to 35°N, the climate in the southern part is warmer than the northern part. Northern Alabama has a warm, humid, temperate climate, and the south has a subtropical climate. Summers are hot and humid with an average high temperature around 33°C; winters are typified by a series of cold fronts. The annual precipitation varies from 150 cm to 162 cm in the northern part and 180 cm to 195 cm in the southern part (Carter & Carter, 1984). Based the inventory data from Alabama Forestry Commission ([www.forestry.state.al.us](http://www.forestry.state.al.us)), 70% of the state is covered by forests. Due to mild climate and heterogeneous landscape, Alabama has great species diversity. The county level is selected in this study because most data are only available at this level.

### *Data*

Butterflies: the butterfly information is from the book of Howell & Charny (2010), which was based

on the year-round field observations from 2001 to 2009 by the authors, their students and colleagues. Photographic survey which is broadly applied for biodiversity research (e.g, McGrath, 2015) was conducted at each county. The spatial resolution of butterfly distribution is at county level, which means the distribution covers the entire county as long as this butterfly species is found at one location. More information can be found in Howell & Charny (2010). In this study, the information of distribution and the average wing size is used.

**Climate:** the climate information is from local weather stations in each county from 2001 to 2009.

**Plants and forest:** the information of plant species diversity in each county of Alabama is from <http://www.alabamaplants.com>. The forest coverage (%) in each county at that time is from Chen (2009).

**Human population:** the human population at each county during the corresponding time period is obtained from Alabama Quick Facts at the USCensus Bureau (<http://quickfacts.census.gov/qfd/index>).

### Statistical method

Standard deviation was used to characterize the fluctuation in air temperature and precipitation in each county. The commonly used least squares technique was used in correlation analysis and T-test of SAS (SAS Institute Inc., NC, USA.). The statistical test was considered significant at  $p < 0.05$ . Data aggregation was applied when the statistical test on individual county data was not significant, but the trend might exist, such as the bin of [0, 10], [11, 20],... [70, 80] was applied for the rank of butterfly species number while testing power-law between the average species number and appeared county number. The butterfly species density in each county was estimated by the total butterfly species number /county area.

## RESULTS

Jefferson County has 79 butterfly species, which is the highest number. The counties with the category of highest butterfly species (50–79) include Madison, Jackson, Tuscaloosa, Jefferson, Ribb, Shelby, and Baldwin (Fig. 1). These counties are

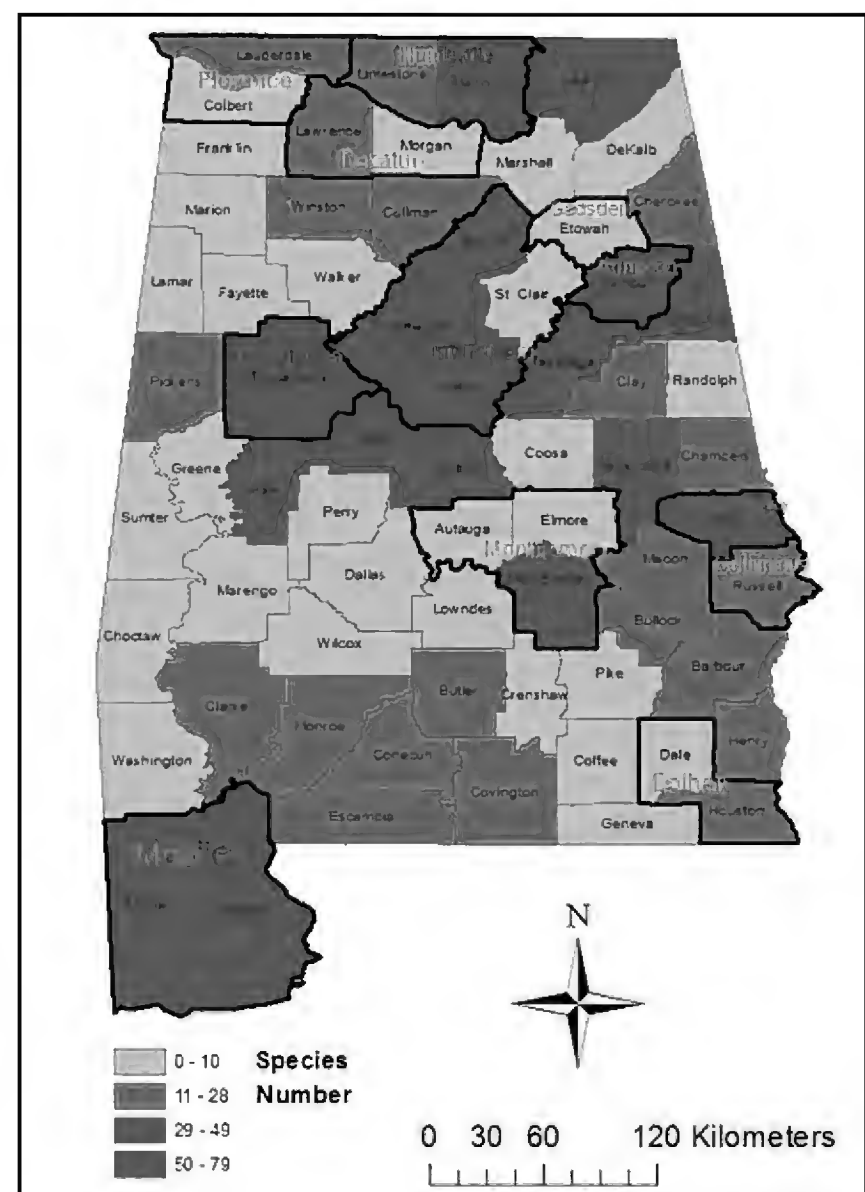


Figure 1. The butterfly distribution across the counties of Alabama (bold lines indicate metropolitan area).

mainly within the metropolitan areas of Huntsville, Birmingham, and Mobile cities. There are six counties (Choctaw, Coffee, Crenshaw, Dale, Greene, and Lamar) without any butterflies or with very limited species number. There is a power-law relationship between the average of butterfly species number and appeared county number (Fig. 2).

The relationship between county size and butterfly species number is not obvious (Fig. 3). The correlation between human population in each county and butterfly species is not significant ( $p > 0.05$ ) (Fig. 4). The relationship between plant species number and butterfly species number among all the counties is not obvious (Fig. 5). There is higher number of butterfly species at areas with either the highest or the lowest forest coverage (Fig. 6).

There is positive correlation between latitude and butterfly species density (Fig. 7). The correlation between the average annual air temperature or average annual precipitation and species density is not significant ( $p > 0.05$ ) (Fig. 8), but there is a general trend of decreased species density with

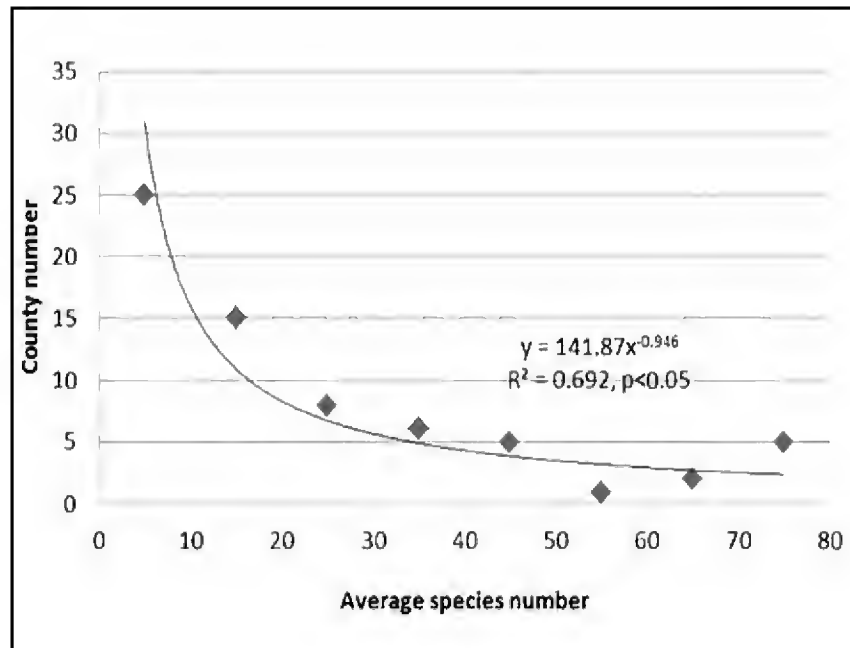


Figure 2. The correlation between average butterfly species number and appeared county number.

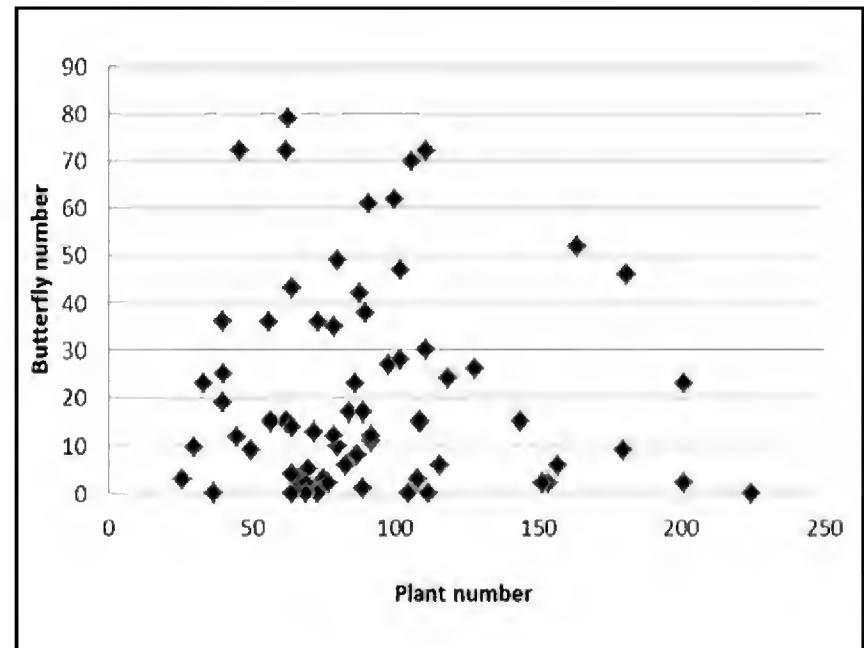


Figure 5. The relationship between plant species number and butterfly species number in counties.

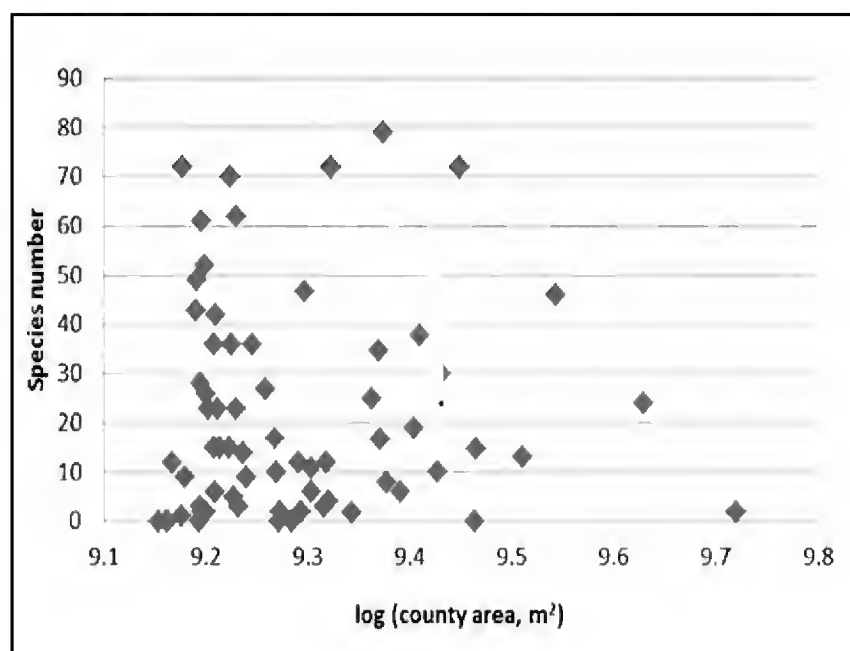


Figure 3. The relationship between county size and butterfly species number.

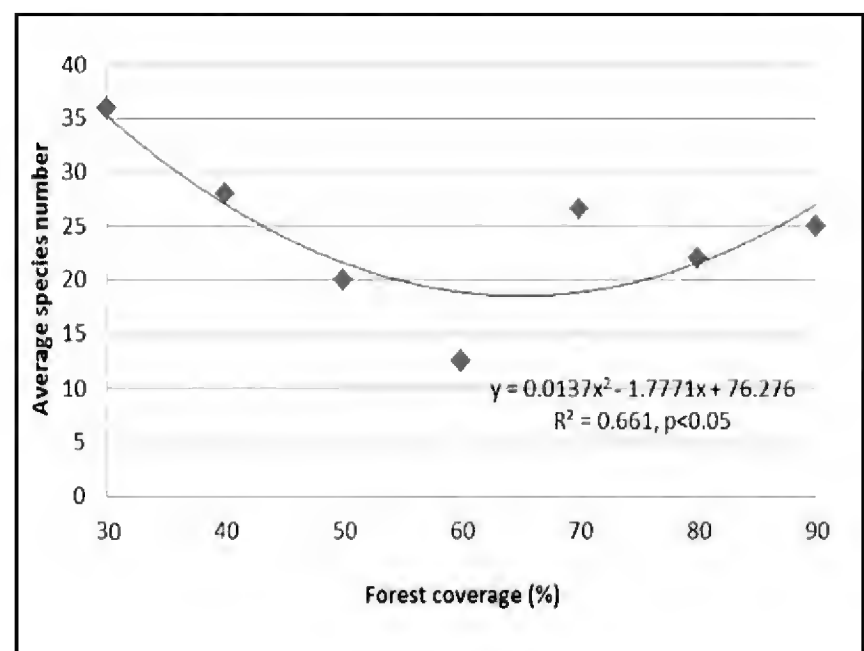


Figure 6. The relationship between forest coverage and butterfly species number in counties.

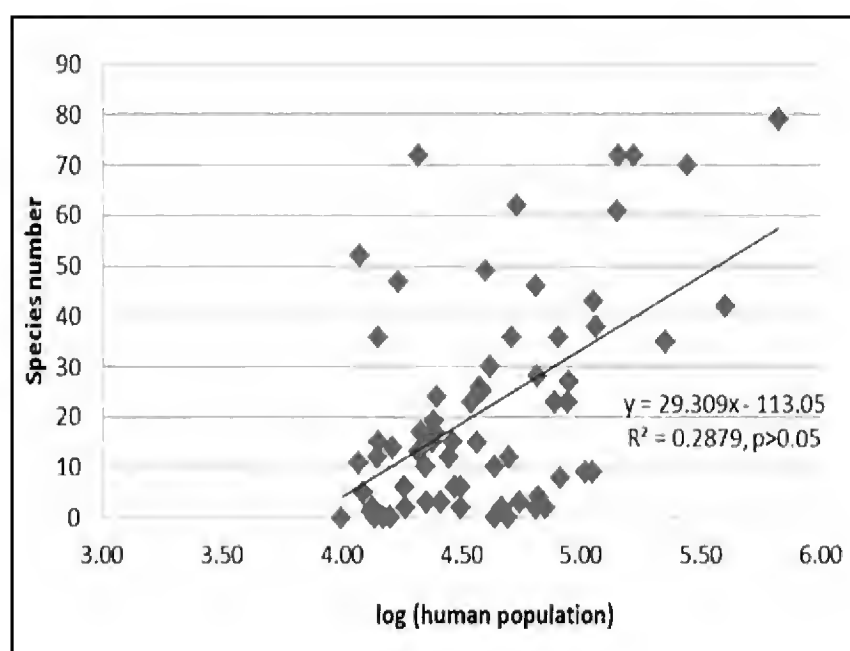


Figure 4. The relationship between human population and butterfly species number among counties.

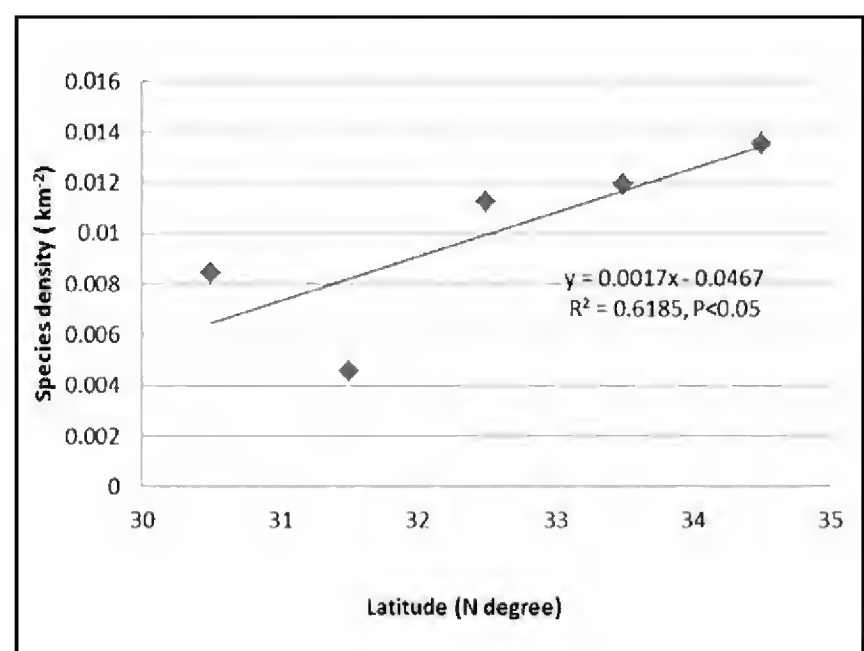


Figure 7. The relationship between latitude and density of butterfly species.

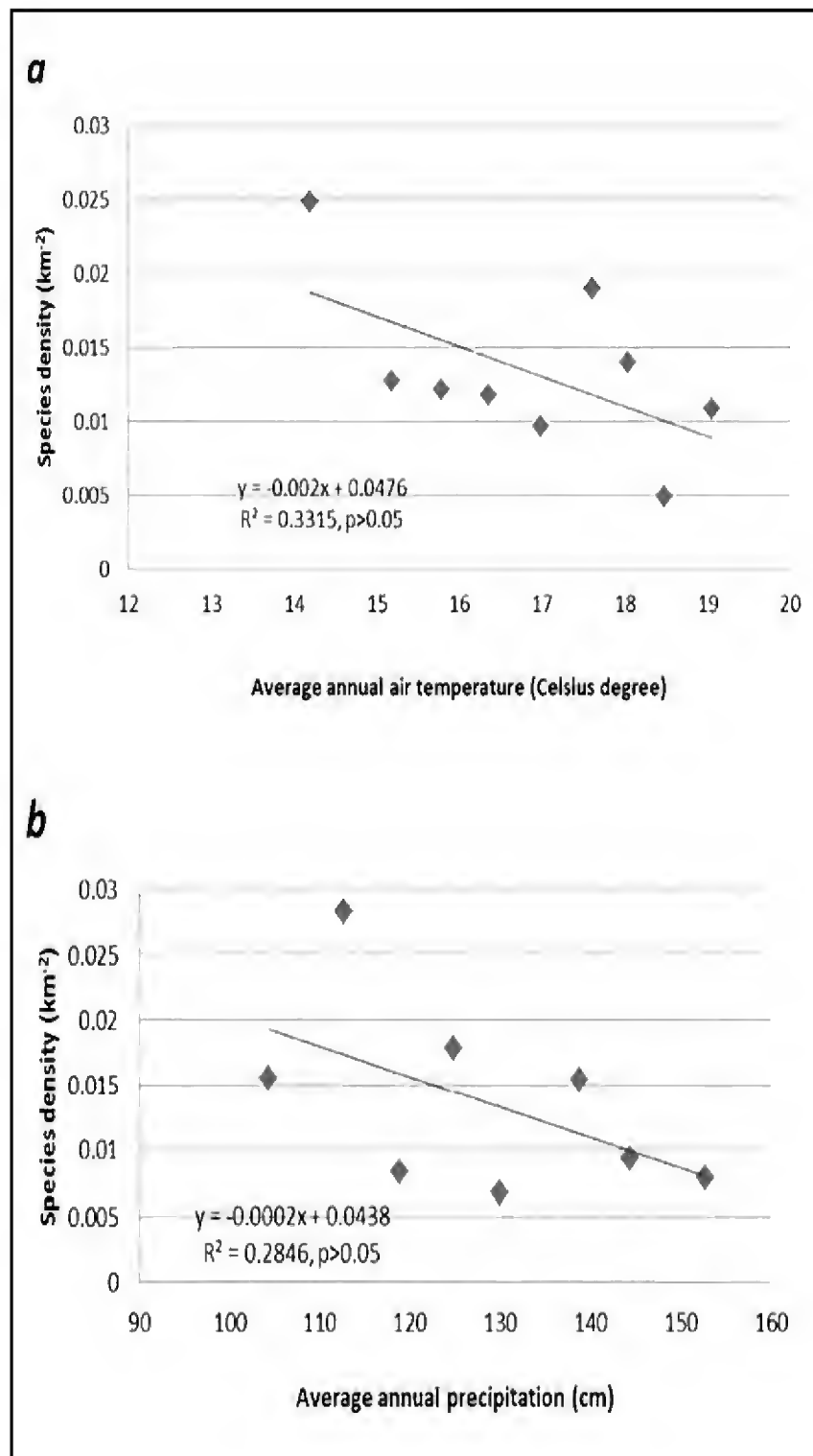


Figure 8. The relationship between butterfly species number and average annual air temperature (a) and average annual precipitation (b).

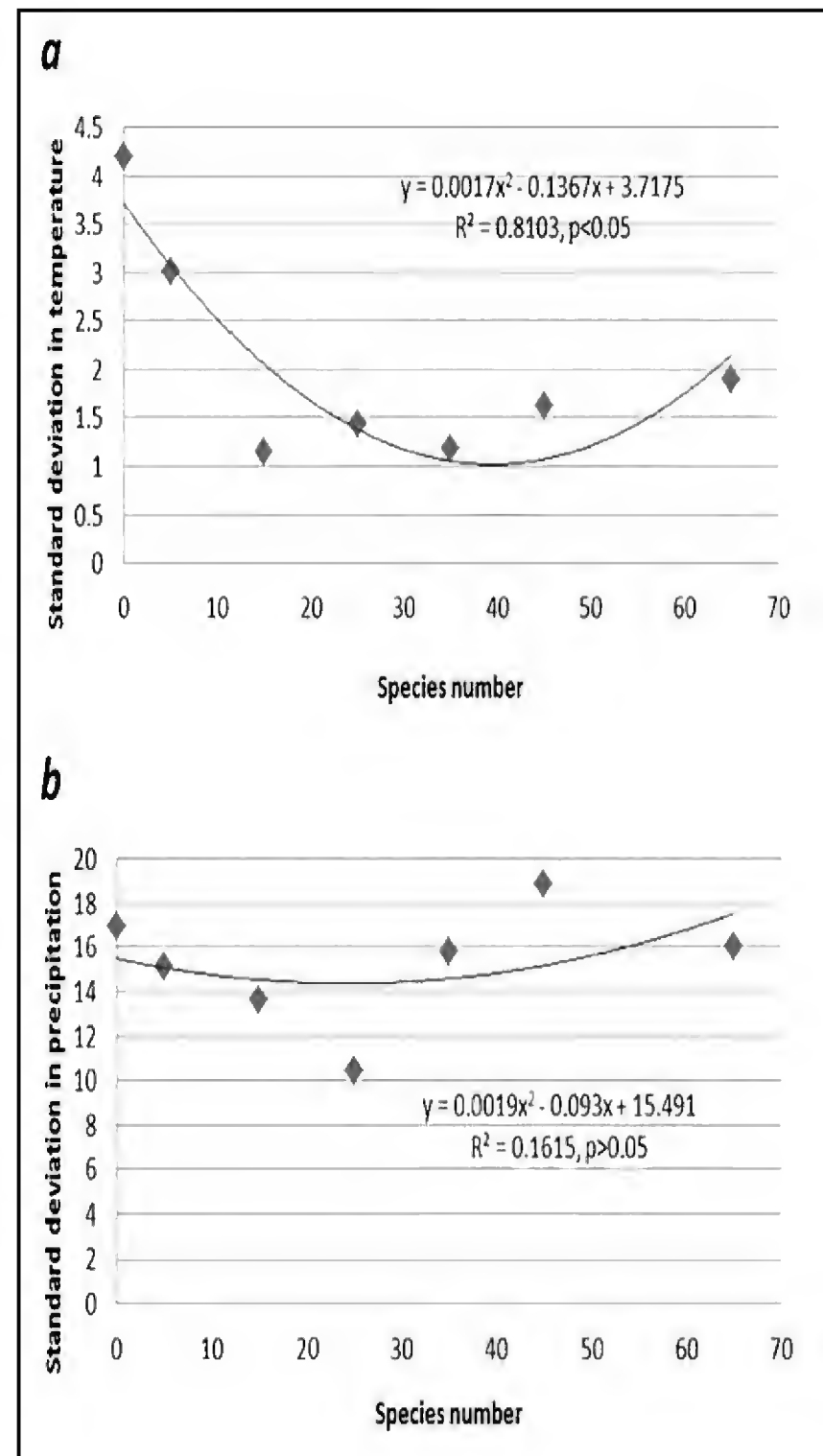


Figure 9. The relationship between butterfly species number and standard deviation of annual air temperature (a) and standard deviation of annual precipitation (b).

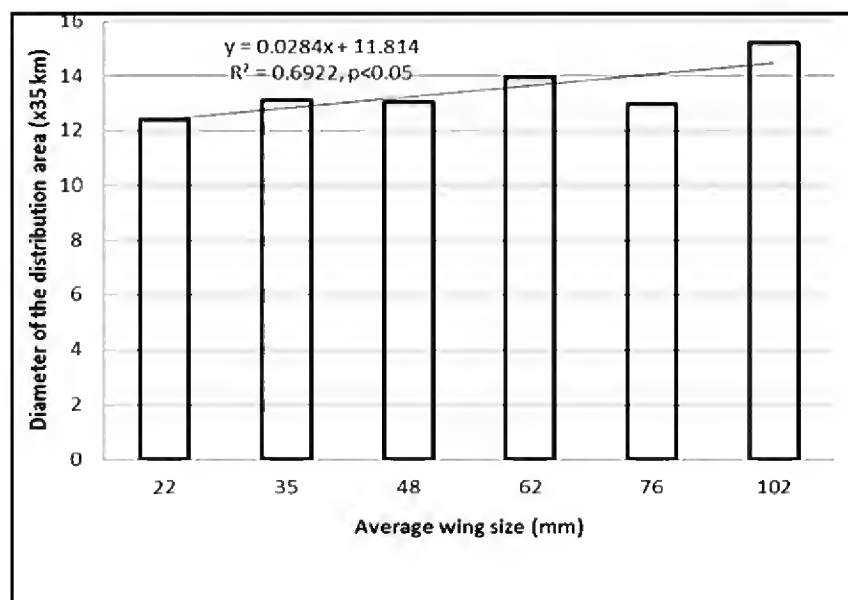


Figure 10. The relationship between average wingsize of butterfly and the diameter of the distribution area.

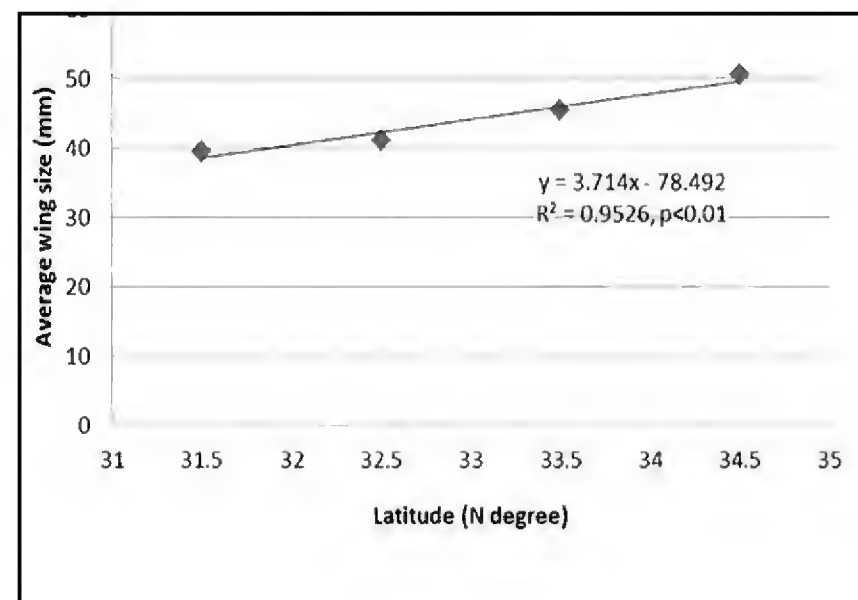


Figure 11. The relationship between latitude and butterfly wingsize.



increased temperature or precipitation. There is a pattern that counties with the lowest or the highest species number have higher standard deviations in annual air temperature or precipitation (Fig. 9).

The correlation between the average wingsize and diameter of distribution area at each county level is not significant ( $p > 0.05$ ). However, after the data aggregation in wingsize, there is a general trend between the average wingsize and the diameter of distribution area (Fig. 10). The average wingsize of the broadly distributed species (or generalists) is  $53.7 \pm 25.7$  mm and  $51.0 \pm 23.7$  mm for narrow distributed species (or specialists). The difference in wing size between generalists and specialists is not statistically significant ( $p > 0.05$ ). With the increase of latitude, the average wingsize increases for all species polled over (Fig. 11).

## DISCUSSION AND CONCLUSIONS

There are some patterns of butterfly distribution in Alabama after the integrated analysis with other information. Some counties have a high species number, but others have limited species. The power-law relationship between average species number and appeared county number is similar to those with plants and animals in California (Chen et al., 2006). The phenomena may be related to the spatial occupying process and tolerance of habitat for all the species, but the mechanism is not known. With the increase of county size in area, this does not necessary lead to the increase in the number of butterfly species, which means big counties may not have more butterfly species. The island biogeography theory does not apply to butterfly species here. The counties with higher number of butterfly species are mainly within these metropolitan areas (e.g., major cities of Birmingham, Huntsville and Mobile areas). It seems that the higher number of butterfly species is related to human population and land use change, although the correlation between butterfly species number and human population in each county is not significant. This is consistent to that (i) no obvious relationship between butterfly species number and plant species number among all counties; (ii) there is high species number at areas with either the lowest or highest forest coverage. After comparing the butterfly species diversity in urban, suburban and rural areas, Mukherjee et al.

(2015) indicated that butterfly species diversity is related to landscape heterogeneity. Usually there is higher landscape heterogeneity at the metropolitan areas due to diverse vegetation pattern under different land uses from land owners, but relatively homogeneity landscape in urban and rural areas. Earlier studies suggested that butterfly diversity is attributed to plant species (Kuussaari et al., 2007). But in this study, there is no obvious correlation between plant species and butterfly species at county level. These butterfly species may only like some specific plants for hosting (Howell & Charny, 2010).

Usually in warmer area, such as tropical areas, there is higher species diversity. However, in this study the relationship between latitude and butterfly species is on the opposite. There is higher density of butterfly species in northern Alabama. This result is also consistent with that there is a general trend of decreased species density with increased temperature. The possible cause may be that the rule at continental (or global) level may not always work at a regional level. Some additional factors may attract to butterfly species diversity at a regional level. Also, in low latitude areas there are high species number as overall, but not necessary for butterfly species.

The results in this study also identify that counties with large fluctuations in annual air temperature and precipitation have either the highest or the lowest species number of butterfly. Under the stable climate condition (e.g., lower standard deviation in annual temperature or precipitation) there is an intermediate high number of butterfly species. The changing climate may provide more niche space for various butterfly species if they can tolerate. The degree to which phenotypic plasticity and adaptation ultimately play a role under this changing climate remains to be further studied (Bowden et al., 2015). Bergmann's rule, describing the relation between latitudinal and body size, is confirmed in this study. Our results indicate that the average wingsize of butterfly increases with the increase of latitude in Alabama.

There are generalists of butterfly with a large distribution area from the south to north and also several specialists with limited distribution in Alabama (such as only one county). But the sizes of their wingspans are not significantly different. This

result may indicate that butterfly species with big wingspans may not necessary show greater migration capacity or the specialists may also be distributed broadly if resource is suitable. The size of wingspan may not determine the fate of some specialist of butterflies under changing environment which was considered as venerable (Dapporto & Dennis, 2013).

After analyzing the records of butterfly species and the environmental factors in Alabama, the emergent patterns at a regional level appear for the distribution of butterfly. The uneven distribution of butterfly species may be related to land use and climate fluctuations. The species diversity and body size related with latitude and temperature may provide helpful information for butterfly conservation and mitigation under climate change. This study may provide a background map for study of butterfly distribution under environmental change (McGrath, 2015). Periodically monitoring the body size and distribution of butterfly species and other biodiversity may be necessary for sustainable regional development.

## ACKNOWLEDGMENTS

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# First record of a Humpback Whale *Megaptera novaeangliae* (Borowski, 1781) in the Tyrrhenian Sea (Cetacea Balaenopteridae)

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## ABSTRACT

It is reported the sighting of a Humpback Whale *Megaptera novaeangliae* (Borowski, 1781) (Cetacea Balaenopteridae) in the Gulf of Pozzuoli, near the coast of Baia (Bacoli, Napoli, Campania, Southern Italy). This record represents the first in the Tyrrhenian Sea, the eighth in the Italian Seas and the twenty-fourth in the Mediterranean Sea.

## KEY WORDS

*Megaptera novaeangliae*; Humpback Whale; sighting; Tyrrhenian Sea.

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## INTRODUCTION

The Humpback Whale, *Megaptera novaeangliae* (Borowski, 1781) (Order Cetacea, Suborder Mysticeti, Family Balaenopteridae) is a cosmopolitan species widely distributed and far-ranging migrant, found in both hemispheres and in all the major ocean basins. During the winter, at the period of mating and calving grounds, all the populations migrate to tropical waters, usually near continental coastlines or island groups; during spring, summer and autumn they move to productive colder waters in temperate and high latitudes, where most of the feeding takes place. In the North Atlantic, during the summer the Humpback Whale ranges from the Gulf of Maine in the West and Ireland in the East, and in the North but not into the pack ice; the northern extent of the Humpback's range includes the Barents Sea, Greenland Sea and Davis Strait (but not the Canadian Arctic), where they occur

mainly in specific feeding areas. During the winter, the majority of whales migrate to wintering grounds in the West Indies, and an apparently small number use breeding areas around the Cape Verde Islands.

In the Mediterranean Sea, the Humpback Whale is not regularly present; in fact it is considered as an irregular or occasional “visitor species”, according to the Reports of Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS), entering the region from the Strait of Gibraltar (Reeves & Notarbartolo di Sciara, 2006; Notarbartolo di Sciara & Birkun, 2010; Cagnolaro et al., 2015). Since 1990 the number of observations has increased and the range of sighting locations has expanded so as to include both basins of the Mediterranean Sea (Frantzis et al., 2004).

Humpback Whale, *Megaptera novaeangliae*, is well known for his long pectoral fins, which can be up to 4.6 meters in length. The dorsal fin is

variable in size and shape, from small triangular knob to larger sickle-shaped, placed nearly two-thirds along back. Head and body are black or grey, white on throat and belly. The adult can measure up to 17 m.

## MATERIAL AND METHODS

We take into consideration the sighting of one individual photographed in the Bay of Pozzuoli; the

sighting occurred from the Aragonese Castle of Baia (District of Bacoli Municipality, Province of Naples) at about 70 m of height. The camera equipment consisted of a Digital single-lens reflex camera Canon EOS 650D with 75-300mmEF-S lens mounted.

## RESULTS AND DISCUSSION

Here we report the sighting of a Humpback

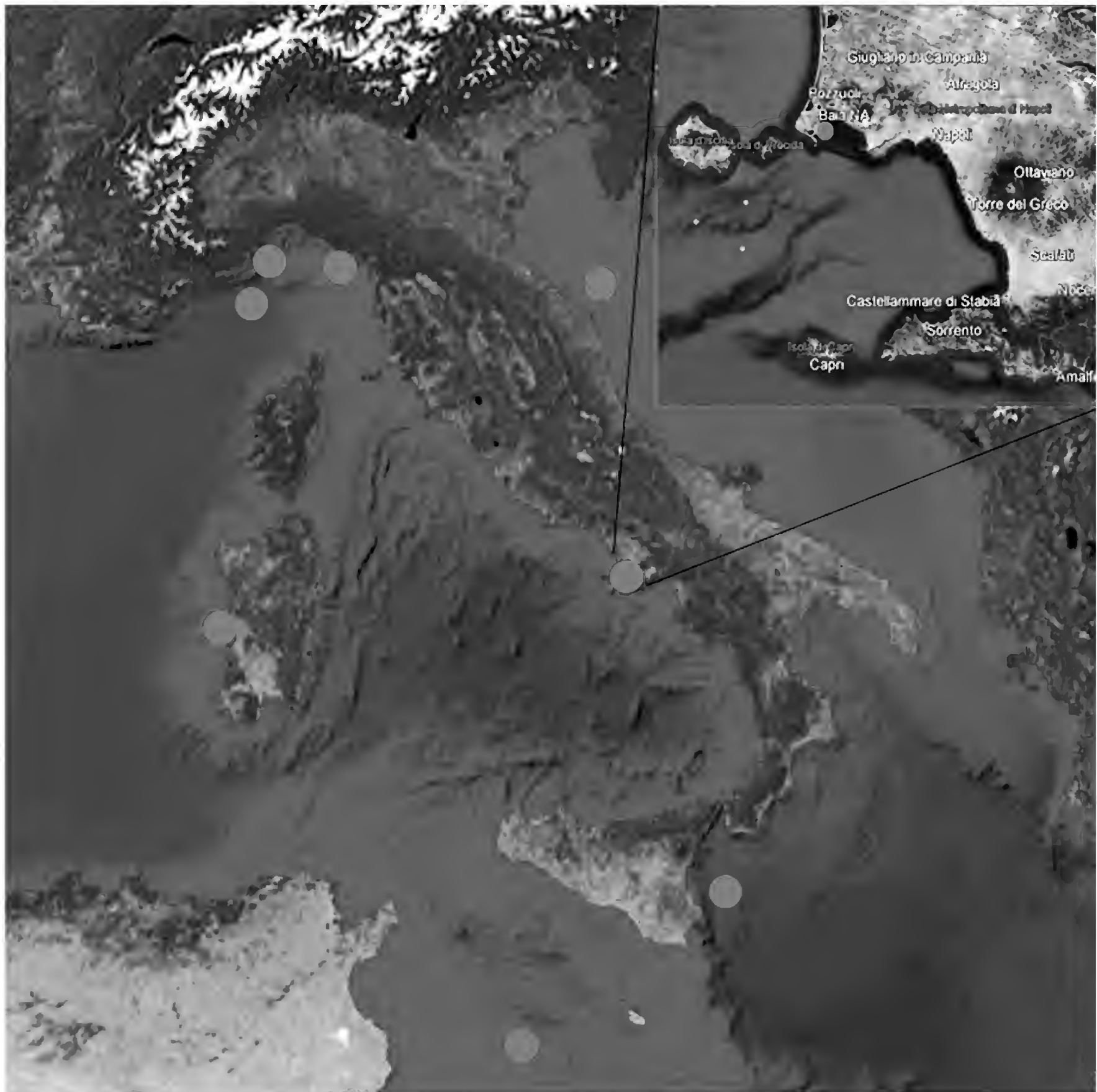


Figure 1. The locations of sightings of Humpback Whales, *Megaptera novaeangliae*, in the Italian Seas.





Figures 2–4. Humpback Whale, *Megaptera novaeangliae*, recorded near Baia, in the Bay of Pozzuoli, apparently in good conditions (Photos by R. Sgammato).

DATE	LOCATION	EVENT	ANIMALS, SIZE	SOURCE AND NOTES
1998, 24 January	Gulf of Oristano (Sardinia) Sardinian Sea	Sighting	1 (7-9 m)	(Frantzis et al., 2004)
2002, 4 August	Senigallia (Province of Ancona, Marche) Adriatic Sea	Sighting	1	(Affronte et al., 2003)
2004, 2 April	Syracuse (Sicily) Ionian Sea	Accidentally by-caught and released	1 (about 10 m)	Centro Studi Cetacei, 2006
2010, 26-28 August	Eastern Ligurian Sea: Versilia (Prov. of Lucca, Tuscany) Sestri Levante (Prov. of Genoa, Liguria)	Repeated sightings of one individual	1 (about 10-13m)	(Cagnolaro et al., 2015)
2011, 24 March	Near Savona (Liguria) Ligurian Sea	Sighting		(Cagnolaro et al., 2015)
2013, 12 March	Lampedusa Island (Sicily) Sicily Channel	Sighting of one individual already observed in French Ligurian Sea	1 (8–9 m)	(Panigada et al., 2014)
2013, August	Ligurian Sea	Sighting of the same individual of Lampedusa	1 (8–9 m)	(Panigada et al., 2014)
2015, 10 December	Baia, Bay of Pozzuoli (Province of Naples, Campania) Tyrrhenian Sea	Sighting	1	Present work

Table 1. Reports concerning specimens of Humpback Whale, *Megaptera novaeangliae*, recorded in the Italian seas.

Whale, *Megaptera novaeangliae*, in the Bay of Pozzuoli near Baia, a District of Bacoli Municipality (Province of Naples, Campania Region) occurred on 10 December 2015. The animal has been observed near the coast at a depth of about six meters, it was approximately 8–9 meters long (probably a juvenile) and with the uppersides of both pectoral fins of white color, apparently in good conditions (Figs. 2–4). This is the first documented record of a Humpback Whale in the Tyrrhenian Sea, and the first sighting for Campania Region (Maio & Quercia, 2006; Maio et al., 2012). Our finding suggests that the Tyrrhenian waters offer suitable habitats also for this species.

Since 1885, 24 records (16 sightings of which four with two individuals, three strandings and 5 by-caught individuals) have been reported from dif-

ferent locations across the Mediterranean basin. All individuals, ranging between 7 and 12 meters, were estimated to be 2–3 years old juveniles (Panigada et al., 2014).

The first occurrence in the Mediterranean Sea was a juvenile caught in 1885 off 15 km West of Toulon (France) (Pouchet, 1885; Beauregard, 1885; Van Beneden, 1889; Aguilar, 1989). Occurrences of Humpback Whales, *Megaptera novaeangliae*, are extremely rare in the Italian Seas being known only six sightings and one captures of single specimens. Date, location and size are given in Table 1. The first occurrence was of a 7–9 m long individual reported in the Gulf of Oristano (Sardinia), in January 1998 (Frantzis et al., 2004).

The last sighting was an individual approximately 8–9 meters long, observed in three different

locations: the first time it was observed in the French Liguria Sea, NW Mediterranean, in June 2012; then, the same animal was re-sighted off Lampedusa Island, Sicily Channel, in March 2013 over 1,000 km away in a straight line from the previous location and again in August 2013, in the “Italian” Ligurian Sea (Panigada et al., 2014). No specimens from Mediterranean Sea are preserved in Italian museums (Cagnolaro et al., 2014).

The Humpback Whale, *Megaptera novaeangliae*, is a species listed in the Appendix I of CITES, and it is considered an “Endangered or threatened species” in the Annex II of the Barcelona Convention for Protection against Pollution in the Mediterranean Sea. It is also included in the Appendix II of the Bern Convention on the Conservation of European Wildlife and Natural Habitats, considered as “Strictly protected fauna species”, and is a “species in need of strict protection” in European Union by the Annex IV of the Council Directive 92/43/EEC of May 21st 1992 on the conservation of natural habitats and of wild fauna and flora, known as “Habitats Directive”. Furthermore the species is classified as “Least Concern” on the IUCN Red List of Threatened Species (vers. 2015.4) (Reilly et al., 2008).

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# Systematic account of Orthoptera fauna of Bastar district, Chhattisgarh, India

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## ABSTRACT

A faunistic survey in Bastar district, Chhattisgarh (India) revealed 52 species belonging to 45 genera, 8 families, including five species which are new record to the Orthoptera fauna of Chhattisgarh: *Calliptamus barbarus barbarus* (Costa, 1836), *Ceracris fasciata* (Brunner von Wattenwyl, 1893), *Oedaleus senegalensis* (Krauss, 1877), *Aularches miliaris miliaris* (Linnaeus, 1758), and *Loxoblemmus haani* Saussure, 1877.

## KEY WORDS

Distribution; Bastar; Orthoptera; Chhattisgarh.

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## INTRODUCTION

The major works on Orthopteran fauna of India were published by Kirby (1914) and Chopard (1969). Notable papers on Orthoptera fauna of Chhattisgarh state were also done by Dwivedi (1978, 1990), Dixit & Sinha (1982), Agrawal & Sinha (1987), Chandra & Gupta (2005), Chandra et al. (2007), Gupta et al. (2008), Gupta & Chandra (2010) and Gupta & Shishodia (2014), but so far no comprehensive account on Orthoptera of Bastar is available a part from a few exceptions including: Chopard (1970) who described *Arachnomimus subalatus* Chopard, 1970 and Sinha & Agrawal (1973) who described *Kempiola shankari* (Sinha et Agrawal, 1973) both from the same locality, i.e. Kutums war cave. Shishodia, (1995) reported 15 species belonging 15 genera under 6 families from Indravati Tiger Reserve, Bastar. Shishodia (2000) reported 77 species of crickets and grasshoppers from Bastar.

## MATERIAL AND METHODS

A total of 514 specimens representing 52 species

belonging 45 genera under 8 families viz. Acrididae 28 species 21 genera, Pyrgomorphidae 4 species 4 genera, Tetrigidae 4 species 4 genera, Tridactylidae 1 species and 1 genus, Gryllidae 6 species 6 genera, Trigonidiidae 2 species 2 genera, Gryllotalpidae 1 species 1 genus, Tettigoniidae 6 species 6 genera, are known from Bastar district of Chhattisgarh. Of these, five species are reported for the first time.

In Table 1 are shown coordinates of collection localities. The species recorded for the first time are marked with an asterisk (\*). All specimens are preserved in collection R.P. Gupta & co-workers collection.

## SYSTEMATIC

Order ORTHOPTERA  
Suborder CAELIFERA  
Superfamily ACRIDOIDEA  
Family ACRIDIDAE  
Subfamily ACRIDINAE  
Genus *Acrida* Linnaeus, 1758



S. No.	Site	Latitude N	Longitude E	Altitude m
1	Asna Village	19°7'15.4"	82°01' 20.9"	539
2	Amaguda	19°9'45.4"	82°0'15.1"	553
3	Bhanpuri	19°19'17.4"	81°51'17.0"	514
4	Bhatiguda Village	19°2'53.4"	82°3'3.5"	515
5	Belguda Village	19°13'03"	81°58'55.1"	552
6	Chidaipadar	19°10'1.7"	81°58'19.9"	543
7	Dongaghatpara	19°00'28.5"	81°05'08"	485
8	Erikpal Village	19°07'17.9"	82°03'34.9"	542
9	Gariya bahar river	19°4'53.2"	82°3'1.9"	547
10	Hathguda	19°5'45.6"	82°3' 9.7"	561
11	Jagdarpur City	19°4'33.4"	82°1'51.7"	478
12	Jeeragaon	19°2'7.9"	82°9'39.1"	563
13	Kalcha	19°6'36.8"	82°6'18.9"	559
14	Kohkapal	19°8'32.1"	82°6'21.4"	562
15	Kolchur	19°10'5.8"	81°57'31.9"	555
16	Kopaguda Village	19°3'34.7"	82°6'43.1"	600
17	Kotamsar	18°52'45"	81°55'21.1"	487
18	Kurundi	19°1'49.5"	82°6'13.1"	578
19	Machkote range	19°0'52.4"	82°8'2.3"	555
20	Malgaon	19°8'6.9"	82°4'47.9"	551
21	Magedha	19°46'0.4"	81°53'16.9"	592
22	Makdi FRH	19°46'22.3"	81°54'12.8"	671
23	Mongrapal Village	19°11'26.9"	81°59'27.1"	572
24	Nakaguda Village	19°10'7.8"	81°2'47.4"	579
25	Neganar Village	19°12'1.7"	81°1'3.3"	488
26	Piplavand	19°19'24.5"	81°55'39.2"	513
27	Pushpal	18°15'23.5"	82°4'53.2"	584
28	Rampal	19°13'39.9"	82°00'41.5"	599
29	Sonarpal beat	19°18'37.5"	81°51'51.5"	486
30	Taraguda	19°9'25"	82°6'17.1"	554
31	Tiwasguda	19°10'3"	82°2'48.5"	579
32	Ulnar	19°10'20.3"	82°7'28"	568
33	Umargaon Village	19°10'40.2"	82°1'36.2"	568

Table 1. Coordinates of collection localities of Bastar district, Chhattisgarh (India).

### 1. *Acrida exaltata* (Walker, 1859)

*Truxalis exaltata* - Walker, 1859: 222

*Acrida exaltata* - Dey & Hazra, 2003: 24

EXAMINED MATERIAL. Chhattisgarh; Bastar, Malgaon, 23.XI.2011, 1 male; 18.IV.2012, 1 male; Belaguda, 16.I.2012, 1 male; Jhariya Bahara Nala, 20.III.2012, 3 males; Kurandi, 23.III.2012, 2 males and 2 females; Erikpal Village, 24.II.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

### 2. *Acrida gigantea* (Herbst, 1786)

*Truxalis gigantea* - Herbst, 1786: 191

*Acrida gigantea* - Joshi et al., 2004: 71

EXAMINED MATERIAL. Chhattisgarh; Bastar, Rampal Village, 19.I.2012, 1 female; Bhanpuri, 20.X.2011, 2 females; Neganar Village, 4.I.2012, 1 male; Dongraghat para, 6.II.2012, 1 male; Jagdarpur city, 13.II.2012, 1 male; Taraguda, 13.II.2012, 4 females; Ericpal Village, 25.II.2012, 1 female; Malgaon, 9.III.2012, 1 female; 10.III.2012, 1 female; Kohkapal, 14.III.2012, 2 females; Kurundi, 23.III.2012, 1 male and 1 female; Gariya Bahar river, 24.III.2012, 1 female; Machkote Range, 7.VI.2012, 2 males and 2 females; Kopaguda, 22.V.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

### 3. *Acrida turrita* (Linnaeus, 1758)

*Gryllus (Acrida) turritus* - Linnaeus, 1758: 427

*Gryllus (Acrida) nasutus* - Linnaeus, 1764: 118

*Acrida turrita* - Kirby, 1914: 98

EXAMINED MATERIAL. Chhattisgarh; Bastar, Mangra para, 7.I.2012, 1 male and 1 female; Belaguda, 18.I.2012, 1 male; Dongaghat para, 7.II.2012, 1 female; 8.II.2012, 1 female; Malgaon, 7.II.2012, 2 males; 10.III.2012, 1 male and 2 females; Erikpal Village, 24.II.2012, 1 female; Kurundi, 23.III.2012, 1 male; Kolchur, 18.IV.2012, 1 male; 7.VI.2012, 1 male; Kopaguda, 22.V.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar and Raipur.

Genus *Phlaeoba* Stål, 1860

4. *Phlaeoba infumata* Brunner, 1893*Phlaeoba infumata* - Brunner, 1893: 124*Phlaeoba infumata* - Dey & Hazra, 2003: 25.

EXAMINED MATERIAL. Chhattisgarh; Bastar, Sonarpal Beat, 17.X.2011, 1 male; Neganar Village, 4.I.2012, 1 male; Nakaguda Village, 24.I.2012, 1 female; Malgaon, 9.II.2012, 1 female; 10.III.2012, 1 male; Erickpal Village, 24.II.2012, 1 male; Kohkapal, 14.III.2012, 3 males and 4 females; Kalcha, 24.IV.2012, 2 males; 18.VI.2012, 1 male; Machkote range, 7.VI.2012, 1 male and 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

5. *Phlaeoba panteli* Bolivar, 1902*Phlaeoba panteli* - Bolivar, 1902: 589*Phleoba panteli* - Dey & Hazra, 2003: 27

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 29.VIII.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily CALLIPTAMINAE

Genus *Calliptamus* Audinet-Serville, 18316. *Calliptamus barbarus barbarus* (Costa, 1836) (\*)*Acridium barbarum* - Costa, 1836: 13*Caloptenopsis punctata* - Kirby, 1914: 208*Calliptamus barbarus barbarus* - Massa, 2009: 81

EXAMINED MATERIAL. Chhattisgarh; Bastar, Amaguda, 24.VIII.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar.

REMARK. New record from Chhattisgarh state.

Subfamily CATANTOPINAE

Genus *Choroedocus* Bolivar 19147. *Choroedocus illustris* (Walker, 1870)*Heteracris illustris* - Walker, 1870: 662, 663*Choroedocus illustris* - Uvarov, 1921a: 109

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 19.VIII.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar.

8. *Diabolocatantops innotabilis* (Walker, 1870)*Acridium innotabile* - Walker, 1870: 629*Diabolocatantops innotabilis* - Jago, 1984: 371

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 29.VIII.2011, 2 females; Neganar Village, 4.I.2012, 1 female; Mograpal Village, 6.I.2012, 2 females; Chidaipadar, 20.I.2012, 1 female; Asna Village, 2.II.2012, 1 female; 4.II.2012, 2 females; Erickpal Village, 24.II.2012, 1 male; Malgaon, 9.III.2012, 2 males and 1 female; Kohkapal, 14.III.2012, 2 females; Gariya bahar river, 22.III.2012, 1 female; Machkote range, 7.VI.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Pachyacris* Uvarov, 19239. *Pachyacris vinosa* (Walker, 1870)*Acridium vinosum* - Walker, 1870: 587*Pachyacris vinosa* - Shishodia & Dey, 2006: 107

EXAMINED MATERIAL. Chhattisgarh; Bastar, Makdi range, 8.XI.2011, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Stenocatantops* Dirsh et Uvarov, 195310. *Stenocatantops splendens* (Thunberg, 1815)*Gryllus splendens* - Thunberg, 1815: 236*Stenocatantops splendens* - Shishodia, 2000: 63

EXAMINED MATERIAL. Chhattisgarh; Bastar, Mograpal Village, 7.I.2012, 1 males and 1 female; Asna Village, 4.II.2012, 1 female; Malgaon, 9.III.2012, 1 male; 10.III.2012, 1male and 3 females; Kohkapal, 14.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Xenocatantops* Dirsh et Uvarov, 195311. *Xenocatantops humilis humilis* (Audinet-Serville, 1839)*Acridium humile* - Audinet-Serville, 1839: 662*Xenocatantops humilis humilis* - Shishodia, 2000: 62

EXAMINED MATERIAL. Chhattisgarh; Bastar, Makdi Pond, 9.IX.2011, 1 female; 7.VI.2012, 1 female; Mograpal Village, 7.I.2012, 1 male; Malgaon, 9.III.2012, 1 male; 9.XII.2012, 1 female; Kohkapal, 14.III.2012, 1 male; Kurundi, 23.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

12. *Xenocatantops karnyi* (Kirby, 1910)

*Catantops karnyi* - Kirby, 1910: 483

*Xenocatantops karnyi* - Shishodia, 2000: 62

EXAMINED MATERIAL. Chhattisgarh; Bastar, Belguda Village, 16.I.2012, 1 female; 18.I.2012, 1 female; Dongaghatpara, 7.II.2012, 1 female; Amaguda, 2.III.2012, 1 male; Malgaon, 10.III.2012, 1 male and 1 female; Kohkapal, 14.III.2012, 1 male and 1 female; Jeeragaon, 26.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar and Raipur.

Subfamily COPTACRIDINAE

Genus *Eucoptacra* Bolivar, 1902

13. *Eucoptacra praemorsa* (Walker, 1870)

*Acridium saturatum* - Walker, 1870: 628

*Eucoptacra saturata* - Uvarov, 1921b: 503

*Eucoptacra praemorsa* - Tandon, 1976: 10

EXAMINED MATERIAL. Chhattisgarh; Bastar, Malgaon, 10.III.2012, 1 female; Taraguda, 16.IV.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily CYRTACANTHACRIDINAE

Genus *Cyrtacanthacris* Walker, 1870

14. *Cyrtacanthacris tatarica* (Linnaeus, 1758)

*Gryllus locusta tataricus* - Linnaeus, 1758: 432

*Cyrtacanthacris tatarica* - Shishodia, 2000: 58

EXAMINED MATERIAL. Chhattisgarh; Bastar, Amaguda, 23.VIII.2011, 1 female; 24.VIII.2011, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily EYEPREPOCNEMIDINAE

Genus *Tylotropidius* Stål, 1860

15. *Tylotropidius varicornis* (Walker, 1870)

*Heteracris varicornis* - Walker, 1870: 667

*Tylotropidius varicornis* - Shishodia, 2000: 60

EXAMINED MATERIAL. Chhattisgarh; Bastar, Belaguda, 18.I.2012, 1 male; Jagdalpur range, 15.VII.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily GOMPHOCERINAE

Genus *Leva* Bolivar, 1909

16. *Leva indica* (Bolivar, 1902)

*Gymnobothrus indicus* - Bolivar, 1902: 596

*Leva cruciata* - Bolivar, 1914: 65

*Leva indica* - Jago, 1996: 94

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 24.VIII.2011, 1 male; Malgaon, 23.XI.2011, 2 males and 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily HEMIACRIDINAE

Genus *Clonacris* Uvarov, 1943

17. *Clonacris kirbyi* (Finot, 1903)

*Euthymia kirbyi* - Finot, 1903: 622–629

*Clonacris kirbyi* - Tandon, 1976: 3

EXAMINED MATERIAL. Chhattisgarh; Bastar, Nakaguda, 19.I.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily OEDIPODINAE

Genus *Aiolopus* Fieber, 1853

18. *Aiolopus thalassinus tamulus* (Fabricius, 1798)

*Gryllus tamulus* - Fabricius, 1798: 195

*Aiolopus thalassinus tamulus* - Shishodia, 2000: 49

EXAMINED MATERIAL. Chhattisgarh; Bastar, Malgaon, 23.XI.2011, 2 males and 1 female; 9.III.2012, 1 female; 10.III.2012, 1 male and 1 female; Jag-

dalpur city, 13.II.2012, 1 female; Ericpal Village, 24.II.2012, 1 female; Kohkapal, 14.III.2012, 3 males and 2 females; Machkote Range, 7.VI.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Ceracris* Walker, 1870

19. *Ceracris fasciata* (Brunner von Wattenwyl, 1893) (\*)

*Parapleurus fasciata* - Brunner von Wattenwyl, 1893: 127

*Rammeacris gracilis* - Willemse, 1951: 66

*Ceracris fasciata* - Ingrisch, 1989: 235

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 29.VIII.2011, 2 females.

DISTRIBUTION IN CHHATTISGARH. Bastar.

REMARK. New record from Chhattisgarh state.

20. *Ceracris nigricornis nigricornis* Walker, 1870

*Ceracris nigricornis* - Walker, 1870: 791

*Ceracris nigricornis* - Kirby, 1914: 110

EXAMINED MATERIAL. Chhattisgarh; Bastar, Taraguda, 16.IV.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Kabirdham, Raipur.

Genus *Gastrimargus* Saussure, 1884

21. *Gastrimargus africanus africanus* (Saussure, 1888)

*Oedaleus (Gastrimargus) marmoratus* var. *Africanus* - Saussure, 1888: 39

*Gastrimargus africanus africanus* - Shishodia, 2000: 51

EXAMINED MATERIAL. Chhattisgarh; Bastar, Kanker, 27.VII.2011, 2 females; Amaguda, 25.VIII.2011, 1 female; Jagdalpur, 29.VIII.2011, 2 females; Asna Village, 2.II.2012, 1 female; Machkote range, 7.VI.2012, 1 male and 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Kabirdham, Raipur.

Genus *Morphacris* Walker, 1870

22. *Morphacris fasciata* (Thunberg, 1815)

*Gryllus fasciatus* - Thunberg, 1815: 230

*Morphacris fasciata sulcata* - Shishodia, 2000: 50

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur city, 29.III.2012, 1 male; Hathguda, 29.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Oedaleus* Fieber, 1853

23. *Oedaleus abruptus* (Thunberg, 1815)

*Gryllus abruptus* - Thunberg, 1815: 233

*Oedaleus abruptus* - Ritchie, 1981: 104

EXAMINED MATERIAL. Chhattisgarh; Bastar, Chitrakot, 25.VIII.2011, 1 female; Nandpur Beat, 20.X.2011, 1 female; Pipalvond, 22.X.2011, 1 female; Ulnar, 22.XI.2011, 1 female; Malegaon, 23.XI.2011, 3 females; 9.III.2012, 1 male and 2 females; 10.III.2012, 8 males and 1 female; Neganar Village, 5.I.2012, 1 female; Mangrapara, 6.I.2012, 1 male; Mograpal Village, 7.I.2012, 1 male and 2 females; Belguda Village, 16.I.2012, 1 female; Rampal, 19.I.2012, 1 female; Asna Village, 2.II.2012, 1 female; 4.II.2012, 2 males; Dongaghatpara, 7.II.2012, 2 females; Erikpal Village, 24.II.2012, 1 female; 25.II.2012, 3 females; Gariya bahar river, 24.III.2012, 1 female; Taraguda, 16.IV.2012, 1 female; Kopaguda, 22.V.2012, 1 male; Machkote range, 7.VI.2012, 1 male; Hathguda, 29.XII.2012, 2 males.

DISTRIBUTION IN CHHATTISGARH. Bastar, Kabirdham Raipur.

24. *Oedaleus senegalensis* (Krauss, 1877) (\*)

*Pachytylus senegalensis* - Krauss, 1877: 56

*Oedaleus senegalensis* - Ritchie, 1981: 94

EXAMINED MATERIAL. Chhattisgarh; Bastar, Kohkapal, 14.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar.

REMARK. New record from Chhattisgarh State.

Genus *Trilophidia* Stål, 1873

25. *Trilophidia annulata* (Thunberg, 1815)

*Gryllus annulatus* - Thunberg, 1815: 234  
*Trilophidia annulata* - Shishodia, 2000: 52

EXAMINED MATERIAL. Chhattisgarh; Bastar, Ulnar, 22.XI.2011, 1 male; Malgaon, 23.XI.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Kabirdham, Raipur.

Subfamily OXYINAE

Genus *Oxya* Audinet-Serville, 1831

26. *Oxya hyla hyla* Audinet-Serville, 1831

*Oxya hyla* - Audinet-Serville, 1831: 287

*Oxya hyla hyla* - Shishodia, 2000: 55

EXAMINED MATERIAL. Chhattisgarh; Bastar, Sonarpal Beat, 17.X.2011, 1 male and 1 female; Ericpal Village, 24.II.2012, 2 females; Malgaon, 9.III.2012, 5 females; Kohkapal Village, 14.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Kabirdham, Raipur.

Subfamily SPATHOSTERNINAE

Genus *Spathosternum* Krauss, 1877

27. *Spathosternum prasiniferum prasiniferum* (Walker, 1871)

*Heteracris prasinifera* - Walker, 1871: 65

*Spathosternum prasiniferum prasiniferum* - Shishodia, 2000: 53

EXAMINED MATERIAL. Chhattisgarh; Bastar, Chitrkote, 23.VIII.2011, 1 male; Nandpur Beat, 20.X.2011, 1 female; Sonarpal Beat, 17.X.2011, 3 males and 1 female; Bhanpuri, 19.X.2011, 1 male; 21.X.2011, 1 female; Asna, 1.XI.2011, 2 females; 4.II.2012, 2 females; Makdi Pond, 9.XI.2011, 2 males and 3 females; Mageda, 9.XI.2011, 1 female; Makdi Range, 11.XI.2011, 1 female; Malgaon, 23.XI.2011, 8 females; 7.III.2012, 1 male; 9.III.2012, 1 male and 4 females; 10.III.2012, 2 males and 5 females; Mograpal Village, 6.I.2012, 1 female; 7.I.2012, 1 female; Belguda Village, 16.I.2012, 1 female; 18.I.2012, 1 female; Rampal Village, 19.I.2012, 1 male; Tiwasguda, 23.I.2012, 1 male; Dongraghat Para, 7.II.2012, 1 female; Taraguda, 13.II.2012, 2 females; 12.III.2012, 2 females; Kohkapal, 14.II.2012, 1 male; Erikpal Village, 24.II.2012, 1 male;

25.II.2012, 1 male; 10.III.2012, 1 male and 4 females; Kohkapal, 14.III.2012, 1 male and 1 female; Ulnar Village, 16.III.2012, 1 male and 1 female; Gariya bahar river, 20.III.2012, 2 males and 6 female; Kurundia, 23.III.2012, 1 male; Jeeragaon, 26.III.2012, 1 male and 1 female; Hatguda, 29.III.2012, 1 male; Taraguda, 16.IV.2012, 3 males and 3 females; Kalcha, 24.IV.2012, 1 male; Bhatiguda, 2.VI.2012, 1 male; Machkote Range, 7.VI.2012, 1 female; Rawanapat, 23.X.2013, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily TERATODINAE

Genus *Teratodes* Brullé, 1835

28. *Teratodes monticollis* (Gray, 1832)

*Gryllus monticollis* - Gray, 1832: 215

*Teratodes monticollis* - Shishodia, 2000: 52

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 29.VIII.2011, 2 females.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Superfamily PYRGOMORPHOIDEA

Family PYRGOMORPHIDAE

Genus *Atractomorpha* Saussure, 1862

29. *Atractomorpha crenulata* (Fabricius, 1793)

*Truxalis crenulata* - Fabricius, 1793: 28

*Atractomorpha crenulata* - Shishodia, 2000: 42

EXAMINED MATERIAL. Chhattisgarh; Bastar, Malgaon, 23.XI.2011, 1 male; 28.VII.2011, 1 female; Daganian, 29.VIII.2011, 1 female; Sonarpara Beat, 17.X.2011, 1 male; Makdi range, 10.XI.2011, 1 male; Neganar Village, 4.I.2012, 1 male; Nathguda Village, 24.I.2012, 1 male; Taraguda, 12.III.2012, 1 male; Ulnar Village, 16.III.2012, 1 male; Kurundi, 23.III.2012, 1 male; Hatguda, 29.III.2012, 1 female; Machkot range, 7.VI.2012, 2 males; Bhatiguda Village, 18.VII.2012, 1 male; Pushpal, 1.VIII.2013, 2 males.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Aularches* Stål, 1873



30. *Aularches miliaris miliaris* (Linnaeus, 1758) (\*)

*Gryllus (Locusta) miliaris* - Linnaeus, 1758: 432  
*Aularches miliaris miliaris* - Mandal & Yadav, 2007: 190

EXAMINED MATERIAL. Chhattisgarh; Bastar, Erikpal Village, 16.VIII.2011, 1 female; Kanker, 27.VII.2011, 1 female; 28.VII.2011, 1 female; Jagdapur city, 29.VIII.2011, 1 female; Jagdlapur range, 30.VIII.2011, 1 female; Asna Village, 2.II.2012, 1 female; Malegaon, 10.III.2012, 1 female; Jhiriya Bahara, 20.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar.

REMARK. New record from Chhattisgarh State.

Genus *Chrotogonus* Audinet-Serville, 1838

31. *Chrotogonus (Chrotogonus) trachypterus trachypterus* (Blanchard, 1836)

*Ommexycha trachypterus* - Blanchard, 1836: 618  
*Chrotogonus (C.) trachypterus trachypterus* - Shishodia, 2000: 40

EXAMINED MATERIAL. Chhattisgarh; Bastar, Amaguda, 24.VIII.2011, 1 male and 1 female; Bhanpur, 19.X.2011, 2 females; 21.X.2011, 1 male and 1 female; Pipalvond Beat, 22.X.2011, 1 male and 1 female; Malegaon, 23.XI.2011, 1 female; Belguda Village, 16.I.2012, 3 females; Natguda Village, 24.I.2012 2 males and 3 females; Neganar Village, 4.I.2012, 1 male; Malegaon, 10.III.2012, 1 female; Kohkapal, 14.III.2012, 1 male and 5 females; Hathguda, 29.III.2012, 1 female; Taraguda, 16.IV.2012, 1 female; Kalcha, 24.IV.2012, 2 males; Ulnar, 22.XI.2011, 1 male and 1 female.

DISTRIBUTION IN CHHATTISGARH. Bstar, Bilaspur, Kabirdham, Raipur.

Genus *Poekilocerus* Audinet-Serville, 1831

32. *Poekilocerus pictus* (Fabricius, 1775)

*Gryllus pictus* - Fabricius, 1775: 289  
*Poekilocerus pictus* - Kirby, 1914: 172

EXAMINED MATERIAL. Chhattisgarh; Bastar, Mo-grapol Village, 7.I.2012, 1 female; Nakaguda, 19.I.2012, 1 male; Amaguda, 2.III.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar and Raipur.

Superfamily TETRIGOIDEA  
 Family TETRIGIDAE  
 Subfamily SCELIMENINAE  
 Genus *Criotettix* Bolivar, 1887

33. *Criotettix bispinosus* (Dalman, 1818)

*Acrydium bispinosum* - Dalman, 1818: 77  
*Criotettix bispinosus* - Bolivar, 1887: 185, 223, 226  
*Criotettix bispinosus* - Gunther, 1938: 134

EXAMINED MATERIAL. Chhattisgarh; Bastar, Sonarpal Beat, 17.X.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar.

Genus *Euscelimena* Gunther, 1938

34. *Euscelimena harpago* (Audinet-Serville, 1839)

*Tetrix harpago* - Audinet-Serville, 1839: 763  
*Euscelimena harpago* - Hebard, 1929: 572

EXAMINED MATERIAL. Chhattisgarh; Bastar, Nakaguda, 19.I.2012, 1 male; Asna Village, 2.II.2012, 2 females; 4.II.2012, 1 female; Malgaon, 10.III.2012, 2 females; Kohkapal, 14.III.2012, 2 females; Machkote Range, 7.VI.2012, 1 male and 1 female; Amaguda, 2.III.2012, 1 male; Kurundi, 23.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily TETRIGINAE  
 Genus *Ergatettix* Kirby, 1914

35. *Ergatettix dorsiferus* (Walker, 1871)

*Tettix dorsifera* - Walker, 1871: 825  
*Ergatettix dorsifera* - Shishodia, 1999: 42

EXAMINED MATERIAL. Chhattisgarh; Bastar, Makdi, 9.XI.201, 1 male; Nakaguda, 19.I.2012, 1 male; Amaguda, 2.III.2012, 1 male; Malgaon, 9.III.2012, 1 male; Ulnar Village, 16.III.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Hedotettix* Bolivar, 1887

36. *Hedotettix gracilis* (de Haan, 1842)

*Acridium (Tetrix) gracile* - de Haan, 1842: 167–169  
*Hedotettix gracilis* - Shishodia, 2000: 36

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 28.VII.2011, 2 males and 1 female; Sonarpali Beat, 17.X.20011, 2 males.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Infraorder TRIDACTYLIDEA  
Superfamily TRIDACTYLOIDEA  
Family TRIDACTYLIDAE Brunner, 1882  
Subfamily TRIDACTYLINAE  
Genus *Tridactylus* Olivier, 1789

37. *Tridactylus thoracicus* Guerin, 1844

*Tridactylus thoracicus* - Guerin, 1844: 336

*Tridactylus thoracicus* - Shishodia & Tandon, 1987: 128

EXAMINED MATERIAL. Chhattisgarh; Bastar, Neganar Village, 5.I.2012, 1 male, DC; 31.I.2012, 1 female, DC; Amaguda, 2.III.2012, 1 female, DC; Gariya bahar river, 24.III.2012, 1 male, DC; Mongrapal Village, 1.I.2012, 1 male, DC; 7.I.2012, 1 female, DC.

DISTRIBUTION IN CHHATTISGARH. Bilaspur and Raipur.

Suborder ENSIFERA  
Infraorder OEDISCHIOIDEA  
Superfamily GRYLLOIDEA  
Family Gryllidae  
Subfamily Gryllinae  
Genus *Loxoblemmus* Saussure, 1877

38. *Loxoblemmus haani* Saussure, 1877 (\*)

*Loxoblemmus haani* - Saussure, 1877: 257

*Loxoblemmus haani* - Vasanth, 1993: 46

EXAMINED MATERIAL. Chhattisgarh; Bastar, Nandpura beat, 20.X.2011, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur.

REMARK. New record from Chhattisgarh State.

Genus *Modicogryllus* Chopard, 1961  
Subgenus *Modicogryllus* Chopard, 1961

39. *Modicogryllus (Modicogryllus) confirmatus* (Walker, 1859)

*Acheta confirmata* - Walker, 1859: 221

*Modicogryllus confirmatus* - Tandon et al., 1976: 170

EXAMINED MATERIAL. Chhattisgarh; Bastar, Nandpura Beat, 20.X.2011, 1 female; Jagdalpur range, 11.XI.2011, 1 female; Gariya bahar river, 20.III.2012, 1 female; Malgaon, 10.III.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Phonarellus* (Gorochoy, 1983)

Subgenus *Phonarellus* Gorochoy, 1983

40. *Phonarellus (Phonarellus) minor* Chopard, 1959

*Gymnogryllus minor* - Chopard, 1959: 1

*Phonarellus (Phonarellus) minor* - Gorochoy, 1983: 323

EXAMINED MATERIAL. Chhattisgarh; Bastar, Bhanpuri, 20.X.2011, 1 female; Mongrapal Village, 7.I.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Teleogryllus* Chopard, 1961

Subgenus *Macroteleogryllus* Gorochoy, 1988

41. *Teleogryllus (Macroteleogryllus) mitratus* (Burmeister, 1838)

*Gryllus mitratus* - Burmeister, 1838: 734

*Teleogryllus mitratus* - Gupta et al., 2008: 120

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 24.VIII.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar and Bilaspur.

Subfamily NEMOBIINAE

Genus *Paranemobius* Saussure, 1877

42. *Paranemobius pictus* (Saussure, 1877)

*Pseudonemobius pictus* - Saussure, 1877: 67

*Paranemobius pictus* - Shishodia, 2000: 70

EXAMINED MATERIAL. Chhattisgarh; Bastar, Neganar Village, 4.I.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar.

Subfamily OECANTHINAE

Genus *Oecanthus* Audinet-Serville, 1831

43. *Oecanthus indicus* Saussure, 1878*Oecanthus indicus* - Saussure, 1878: 454.*Oecanthus indicus* - Shishodia, 2000: 71

EXAMINED MATERIAL. Chhattisgarh; Bastar, Ericpal Village, 24.II.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar and Bilaspur.

Family TRIGONIDIIDAE

Genus *Anaxipha* Saussure, 187444. *Anaxipha* sp.*Anaxipha* - Saussure, 1874: 370*Anaxipha* - Vasanth, 1993: 108

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur Forest, 15.VII.2011, 1 male and 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Trigonidium* Rambur, 1839Subgenus *Trigonidium* Rambur, 183945. *Trigonidium (Trigonidium) cicindeloides* Rambur, 1839*Trigonidium cicindeloides* - Rambur, 1839: 39*Trigonidium cicindeloides* - Shishodia, 2000: 74

EXAMINED MATERIAL. Chhattisgarh; Bastar, Bhanpuri, 19.X.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Raipur.

Family GRYLLOTALPIDAE

Genus *Gryllotalpa* Latreille, 180246. *Gryllotalpa africana* Beauvois, 1805*Gryllotalpa africana* - Palisot de Beauvois, 1805: 229*Gryllotalpa africana* - Shishodia, 2000: 64

EXAMINED MATERIAL. Chhattisgarh; Bastar, Nandpura Village, 20.X.2011, 1 male; Bhanpur, 21.X.2011, 1 male; Rampal, 19.I.2012, 1 female; Hathguda, 29.III.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Superfamily TETTIGONIOIDEA

Family TETTIGONIIDAE

Subfamily CONOCEPHALINAE

Genus *Conocephalus* Thunberg, 1815Subgenus *Anisoptera* Latreille, 182947. *Conocephalus (Anisoptera) maculatus* (Le Guillou, 1841)*Xiphidion maculatum* - Le Guillou, 1841: 294*Conocephalus maculatus* - Chandra et al., 2007: 2684

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur Forest, 15.VII.2011, 1 female; Bhanpuri Forest, 20.X.2011, 1 female; Mangrapal Village, 7.I.2012, 2 females; Belguda Village, 16.I.2012, 1 female; 18.I.2012, 1 female; Naganar Village, 31.I.2012, 1 male; Asna Village, 4.II.2012, 1 female; Dongaghat, 8.II.2012, 1 female; Amaguda Village, 2.III.2012, 1 male; Malegaon, 10.III.2012, 1 female; Jagdalpur, 12.III.2012, 1 male; Taraguda, 12.III.2012, 1 male; Bhanpuri, 15.III.2012, 1 female; Bhatiguda Village, 2.VI.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily MECOPODINAE

Genus *Mecopoda* Audinet-Serville, 183148. *Mecopoda elongata elongata* (Linnaeus, 1758)*Gryllus (Tettigonia) elongatus* - Linnaeus, 1758: 429*Mecopoda elongata* - Barman, 2003: 195

EXAMINED MATERIAL. Chhattisgarh; Bastar, Taraguda, 16.IV.2012, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily PHANEROPTERINAE

Genus *Elimaea* Stål, 1874Subgenus *Orthelimaea* Karny, 192649. *Elimaea (Orthelimaea) securigera* Brunner von Wattenwyl, 1878*Elimaea (Orthelimaea) securigera* - Brunner von Wattenwyl, 1878: 93*Elimaea (Orthelimaea) securigera* - Barman, 2000: 264

EXAMINED MATERIAL. Chhattisgarh; Bastar, Kotamsur, 27.VII.2011, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Genus *Himertula* Uvarov, 1940

50. *Himertula kinneari* (Uvarov, 1923)

*Himerta kinneari* - Uvarov, 1923: 661

*Himertula kinneari* - Ingrisch & Shishodia, 2000: 20

EXAMINED MATERIAL. Chhattisgarh; Bastar, Jagdalpur range, 30.VIII.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar and Raipur.

Genus *Phaneroptera* Audinet-Serville, 1831

Subgenus *Phaneroptera* Audinet-Serville, 1831

51. *Phaneroptera gracilis* Burmeister, 1838

*Phaneroptera gracilis* - Burmeister, 1838: 690

*Phaneroptera gracilis* - Shishodia, 1999: 36

EXAMINED MATERIAL. Chhattisgarh; Bastar, Eripal, 24.II.2012, 1 male.

DISTRIBUTION IN CHHATTISGARH. Bastar, Bilaspur, Raipur.

Subfamily Pseudophyllinae

Genus *Sathrophyllia* Stål, 1874

52. *Sathrophyllia rugosa* (Linnaeus, 1758)

*Gryllus (Tettignonia) rugosa* - Linnaeus, 1758: 430

*Sathrophyllia rugosa* - Beier, 1962: 199–200

EXAMINED MATERIAL. Chhattisgarh; Bastar, Eripal, 22.VII.2011, 1 female.

DISTRIBUTION IN CHHATTISGARH. Bastar, Raipur.

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# First record of *Brachytron pratense* (Müller, 1764) in Sicily (Odonata Aeshnidae)

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## ABSTRACT

*Brachytron pratense* (Müller, 1764) is a small Odonata Aeshnidae widespread throughout most of Europe and Central-northern Italy, but up to now never recorded in Sicily. During the spring 2015, some specimens of this species were observed and photographed for the first time at the swamp lake “Pantano Cuba”, in the southeast coast of Sicily, near to Pachino (Syracuse). This record represents now the southernmost Italian locality for this species.

## KEY WORDS

Pantano Cuba; Odonata; dragonflies; Stiftung Pro Artenvielfalt; Sicily.

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## INTRODUCTION

*Brachytron pratense* (Müller, 1764) is a small Odonata Aeshnidae that is often confused with others species belonging to the genus *Aeshna* Vander Linden, 1820; however, unlike these, it can be observed in flight early in March and it presents some peculiar morphological characters. It is a generally localised species, with a Central European distribution which extends to Balkan and Mediterranean region. Its range includes the west of the Urals, France (Corsica included), Netherlands, Ireland, United Kingdom, Switzerland, Austria, Germany, Slovenia, Croatia, Czech Republic, Slovakia, Greece, Denmark, Finland, Norway, Sweden, Poland, Romania, Estonia, Latvia, Lithuania, Belarus and Russia (Askew 2004; Dijkstra & Lewington, 2006).

In Italy it is an uncommon species and appears more widespread in northern regions, with the

exception of Liguria and Val D'Aosta (Fig. 1). However, in the central and southern regions only few isolated localities are known, so that a good definition of areal borders is precluded (Riservato et al., 2014a). Until now the species had never been reported for Sicily (Riservato et al., 2014b) and the known southernmost record was in Calabria, near Lamezia Terme (Fig. 1). Therefore, this new record extends southward the known Italian distribution of this species and represents now its southernmost Italian locality.

## MATERIAL AND METHODS

During a biodiversity monitoring program promoted by the German "Stiftung Pro Artenvielfalt - Pro Biodiversity Foundation" at the swamp lake “Pantano Cuba”, since April 2015 we have observed and photographed some specimens of *B.*

*pratense*. Data were collected during odonatologic surveys from March 2015 to December 2015. Surveys have been conducted regularly every week at the same location and with the same method: transects traversed on foot, collecting and releasing the specimens with aerial nets for identification. Moreover several macrophotos have been made on-site using a digital SLR camera.

The species shows characters so unmistakable that it was not necessary to kill and preserve the

specimens captured. So they were released immediately after the identification.

The place of occurrence, Pantano Cuba (36°42'26.71"N; 15°1'39.15"E), along a complex of others 7 swamp lakes with different sizes, constitute a very important coastal wetland which was part of a natural reserve named "Riserva dei Pantani della Sicilia Sud-orientale" (Fig. 2), whose establishment was cancelled on May 2015. The swamp, which is located less than 500 meters from the sea, lies entirely in the municipality of Pachino, in the province of Syracuse; it has an extension of 63 hectares and it is characterized by brackish and still waters with abundant aquatic vegetation represented mainly by *Ruppia maritima* L., vegetation helophytic with *Phragmites australis* (Cav.), *Bolboschoenus maritimus* (L.) Palla, *Juncus acutus* L., *Juncus maritimus* Lam. and *Tamarix africana* Poir., as well as by halophytic vegetation zones with *Arthrocnemum fruticosum* (L.) and *Inula crithmoides* L. Near to the swamp shores there are also idle land, now entirely covered by grassy vegetation and several trees of *Acacia saligna* Labill.

## RESULTS

*Brachytron pratense* adults have a length of 54–63 mm and a wingspan of 68–74 mm. They are unmistakable, characterized by hairy thorax and abdomen, densely covered by thin setae (Figs. 3–6). The sides of thorax are green, distinctly interrupted by two complete black lines (Fig. 3). The wings with a narrow and elongated pterostigma (Fig. 4). Males abdomen black and cylindrical, not narrowed at the base, with pairs of elongated blue spots on almost all segments and a diagnostic central yellow dot on the first abdominal tergite S1 (Figs. 4, 6). The females (Figs. 3, 5) are similar to males, except for abdomen stout, browner with greenish-yellow (not blue) spots (Askew, 2004; Dijkstra & Lewington, 2006).

During the surveys at Pantano Cuba, several specimens of *B. pratense* were observed in at least four different occasions, always in the same site; they were adults of both sexes:

- April 9, 2015, 1 female (Figs. 3, 5): it was caught near one of the fallow fields, about 60 meters from the main water body; it was photographed and released.

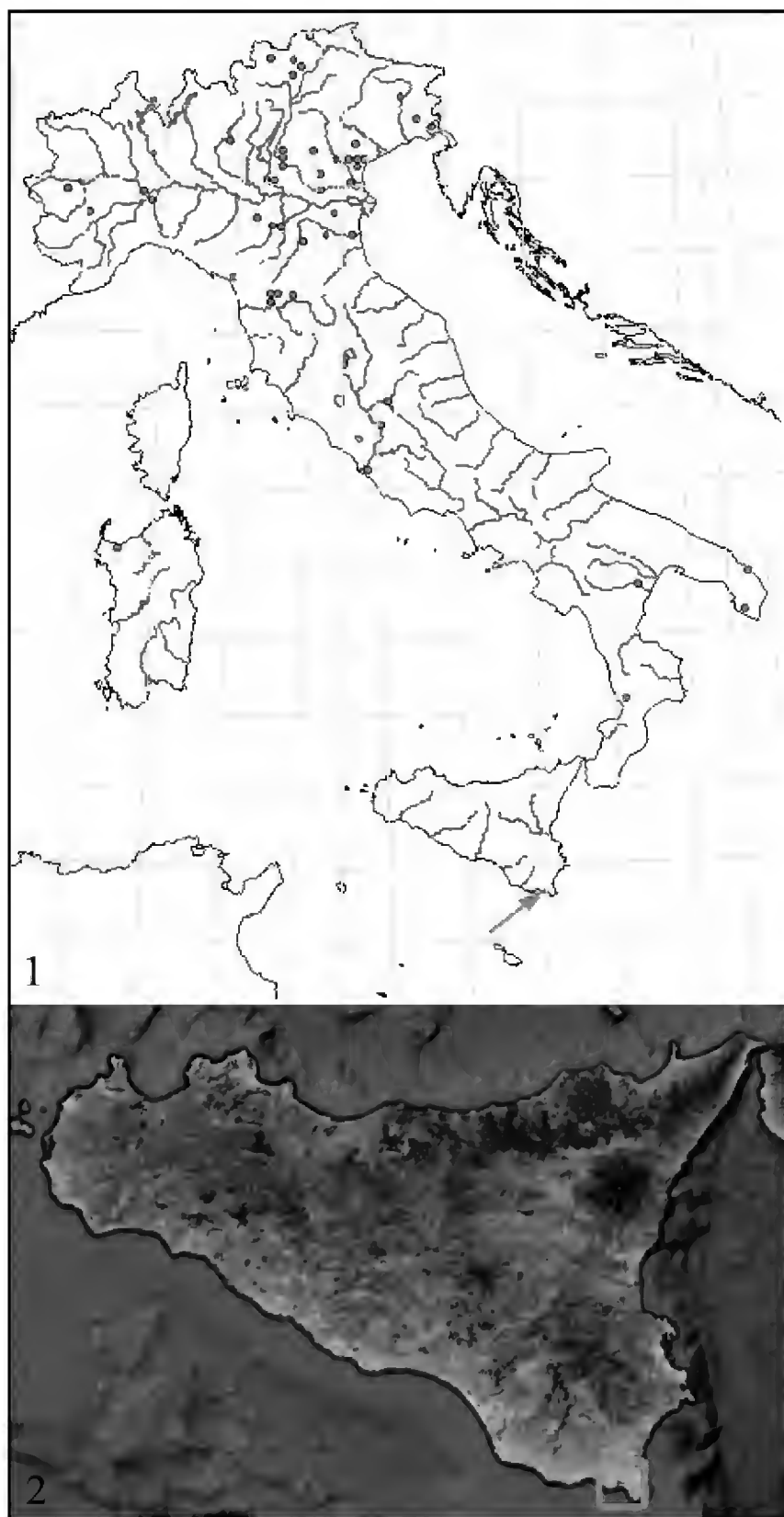


Figure 1. Distribution map of *Brachytron pratense* in Italy. Red arrow shows the new record area (edit from CKmap). Figure 2. Location of "Riserva dei Pantani della Sicilia sud-orientale" (Pachino, Syracuse), new locality record for *Brachytron pratense* (from Google Earth).



Figures 3. *Brachytron pratense* female (Pachino, Pantano Cuba; 9.IV.2015): in hand (ventral-lateral view), showing the typical hairy body. Figure 5. Dorsal view of the same specimen. Figure 4. *Brachytron pratense* male (Pachino, Pantano Cuba; 1.V.2015): dorsal view (pt, pterostigma). Figure 6. *Brachytron pratense* male (Pachino, Pantano Cuba; 23.IV.2015): dorsal-lateral view (Photos by P. Galasso).

- April 23, 2015, 1 male (Fig. 6): it was observed and photographed on a branch of *Acacia saligna* near a small ditch about 130 meters from the main water body.

- May 1, 2015, 2 males: they showed territorial behaviour, one of them was photographed (Fig. 4); they were observed in a wet meadow of *Inula crithmoides* a few meters from the main water body.

- May 7, 2015, 1 male (not photographed): it was observed in full predatory activities through

open meadows about 100 meters from the main water body.

## CONCLUSIONS

These records add an important and valuable contribution to the Italian and European odonatology and especially to the study of *B. pratense* distribution and ecology.

Pantano Cuba is the first sicilian site for this species and the southernmost of Italy and Europe; it also highlights the undoubted importance of research projects and monitoring of high conservation value areas such as the Pantano Cuba, often underestimated and not subject to the strict retention policies and management of biodiversity which they would deserve.

#### ACKNOWLEDGEMENTS

We wish to thank “ODONATA.IT - Società Italiana per lo Studio e la Conservazione delle Libellule” (Carmagnola, Torino, Italy), for further confirmation of identification through the analysis of the photographic material.

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# First record of *Callistochiton pachylasmae* (Monterosato, 1879) for the Adriatic Sea (Polyplacophora Callistoplacidae)

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## ABSTRACT

It is reported the first record of *Callistochiton pachylasmae* (Monterosato, 1879) for the Adriatic Sea. It is a very rare and peculiar polyplacophoran species (Callistoplacidae Pilsbry, 1893). Actually, the few known records span a wide Mediterranean range and extend to the neighbouring Atlantic.

## KEY WORDS

*Callistochiton pachylasmae*; polyplacophoran species; first record; Adriatic Sea.

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## INTRODUCTION

*Callistochiton pachylasmae* (Monterosato, 1879) (original combination: *Chiton pachylasmae* Monterosato, 1879 ex Seguenza G. ms) is a very peculiar polyplacophoran species (Callistoplacidae Pilsbry, 1893; Bouchet et al., 2016; Gofas & Le Renard, 2016), easily recognizable by its peculiar sculpture, in particular for the presence of 7 radial ridges on the cephalic plate. Its distinctiveness, along with its apparently isolated fossil history in Europe, traced back to at least the Pleistocene (Dell'Angelo et al., 1998), brought Dell'Angelo & Oliverio (1997) to allocate it in a subgenus on its own: *Allerychiton* Dell'Angelo et Oliverio, 1997.

## DISCUSSION AND CONCLUSION

*Callistochiton pachylasmae* is a rare species, and it has been treated seldom in the literature (Monterosato, 1879; Sabelli, 1971; Ferreira, 1979;

Kaas, 1981; van Belle, 1983, 1988; Gagliani, 1985; Pizzini & Oliverio, 1993; Giovine & Dell'Angelo, 1993; Kaas & van Belle, 1994; Dell'Angelo & Oliverio, 1997; Dell'Angelo et al., 1998; Antoniadou et al., 2005; Koukouras, 2010). The few known records span a wide Mediterranean range and extend to the neighboring Atlantic (Fig. 1). It is noteworthy that the generic record from Spain in the Iberian Fauna Databank (Ramos, 2010) could not be linked to an actual, published record (J. Templado, pers. comm.) and therefore could not be plotted in the map (Fig. 1). However, despite the wide range, there was so far remarkable lack of findings in the Adriatic Sea.

The present record consists of a single cephalic plate, 0.82 x 1.37 mm (Fig. 2), retrieved by sorting a sample of bioclastic sediment with limited organogenous component, collected by SCUBA diving at Lastovo Island (Croatia), 38 m depth (Alessandro Raveggi, Florence, legit). This is the first record from the Adriatic Sea, and represents the northernmost known record for the species.

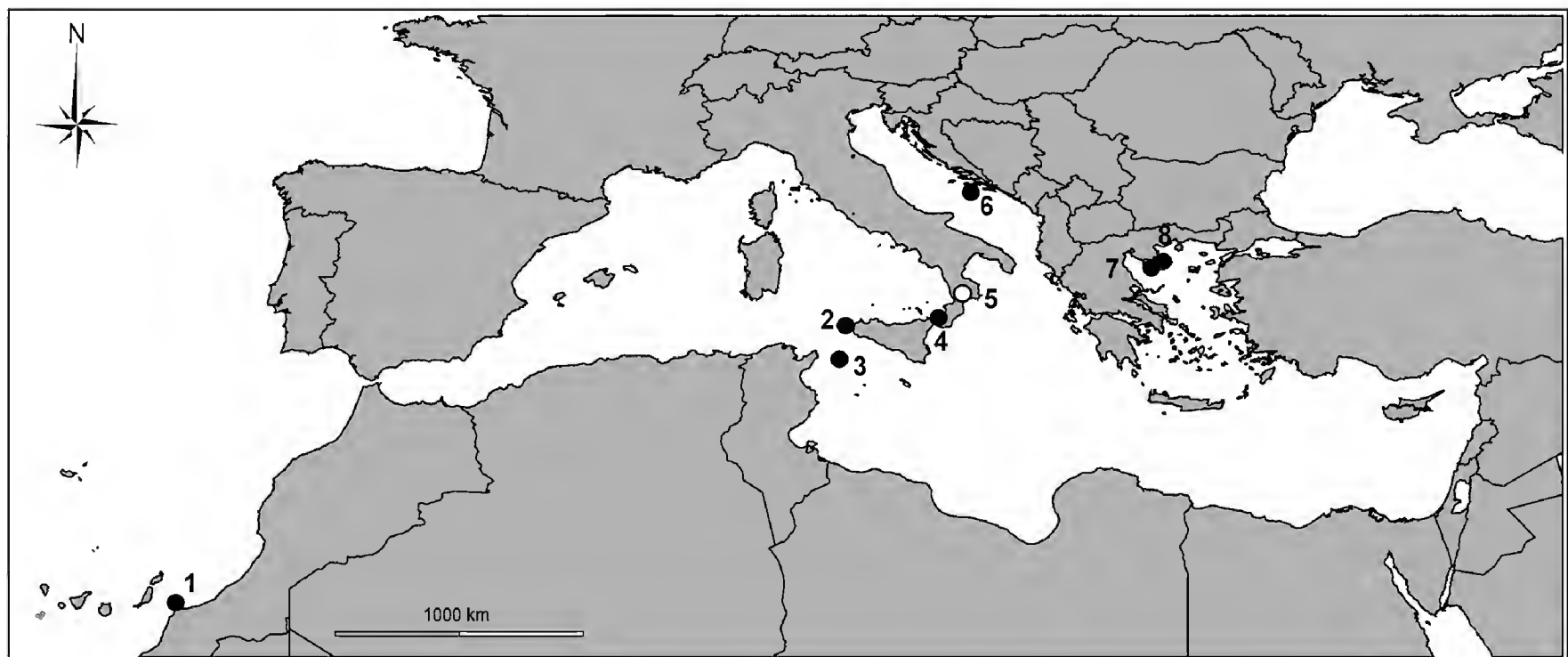


Figure 1. Known records of *Callistochiton pachylasmae* (Monterosato, 1879). 1) W of Cape Yubi, Morocco, -500 m, 1 specimen now lost (Kaas, 1981). 2) Punta Longa “Secca Galera”, Favignana Island -33 m, 1 cephalic plate (Dell’Angelo & Oliverio, 1997). 3) Pantelleria Island, -53.4 m (Pizzini & Oliverio, 1993). 4) Strait of Messina, coralligenous, 1 specimen (holotype: Monterosato, 1879). 5) S. Maria di Catanzaro, Pleistocene, 1 cephalic plate (Dell’Angelo et al., 1998). 6) Lastovo Island (Croatia), -38 m (this work). 7) Kelyfos Island, -30 m, 1 specimen (Antoniadou et al., 2005; Koukouras, 2010). 8) Ormos Panagias -35/40 m, Sithonia, 1 intermediate plate (Dell’Angelo & Oliverio, 1997).



Figure 2. *Callistochiton pachylasmae* (Monterosato, 1879). Lastovo Island (Croatia), 38 m depth. Cephalic plate, height 0.82, width 1.37 mm.

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## ***Jujubinus errinae* n. sp. (Gastropoda Trochidae) from the Strait of Messina, Mediterranean Sea**

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### **ABSTRACT**

A new species of the gastropod family Trochidae, *Jujubinus errinae* n. sp., from the Mediterranean Sea is described based on shell characters. The new taxon was compared with the most closely related species showing marked sculpture and from relatively deep water habitat, *J. catenatus* Ardovini, 2006, *J. montagui* (Wood, 1828) and *J. tumidulus* (Aradas, 1846). The species, which is known from the type locality only, the Strait of Messina, might be strictly associated to the endemic hydrocoral *Errina aspera* (Linnaeus, 1767) beds (Hydrozoa Stylasteridae).

### **KEY WORDS**

Trochidae; Recent; *Jujubinus errinae*; new species; Mediterranean Sea.

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### **INTRODUCTION**

The Strait of Messina has been considered a separate Mediterranean biogeographic microsector inhabited by rich benthic communities and some peculiar assemblages that are unknown in other Mediterranean regions (Bianchi, 2004). From this specific area, a survey of the species of the genus *Jujubinus* Monterosato, 1884 (Gastropoda Trochidae) has been carried out on samples from hard and soft circalittoral bottoms, which revealed the presence of trochidae shells not recognizable as a known species. The specimens, once compared with *Jujubinus catenatus* Ardovini, 2006, *J. montagui* (Wood, 1828) and *J. tumidulus* (Aradas, 1846), the most closely related species showing marked sculpture and from relatively deep water habitat, were attributed to a new species of this genus, *J. errinae*

n. sp., which is here described.

**ACRONYMS.** The materials used for this study are deposited in the following private and Museum collections: Carlo Smriglio and Paolo Mariottini, Rome, Italy (CS-PM); DiSBA Benthic Ecology laboratory Messina, Italy (DiSBA); Giuseppe Notaristefano, Messina, Italy (GN); Museo Civico di Zoologia, Rome, Italy (MCZR); Museo di Zoologia Bologna, Bologna, Italy (MZB); Renato Marconcini, Reggio Calabria, Italy (RM); Walter Renda collection, Reggio Calabria, Italy (WR); Bruno Amati, Roma, Italy (BA); Ermanno Quaggiotto, Logare, Vicenza, Italy (EQ). Other acronyms used in the text: Height (H); Interdepartmental Laboratory of Electron Microscopy, Rome, Italy (LIME); Monterosato (MTS); Scanning Electron Microscopy (SEM); specimens (sps); station (st); Width (W).

## MATERIAL AND METHODS

Hard and soft bottom samples containing the new species were collected in the Strait of Messina, central Mediterranean, in several cruises sponsored by the University of Messina. In particular, dredging was carried out during the “POP 95” cruise (13 to 31 July 2015), at 100 m depth (DG04: 38°14'45" N, 15°37'36" E), and arising from 115 m to 90 m, along a steep rocky floor (DG001: 38°14'45" N, 15°37'28" E).

During the same cruise, van Veen grab samples were collected in Rada Paradiso [Station (St) 02: 38°13'27"N, 15°36'02"E], 201 m depth. A further grab sample, collected by the R/V *Coopernaut Franca* in the framework of the POR-CAL 2008 project, was carried out in October 2008, on the slope of the Gioia Basin (St 1B: 38°18'6941N, 15°45'5710E), 371 m depth. Bioclastic sediment samples were also collected during SCUBA diving on the bottoms of the Strait of Messina, at a depth of 40–50 m (38°15'36"N, 15°43'08"E). Sediment samples were sieved through a 1 mm mesh and the residue was sorted using a stereomicroscope. Among the sorted material, shells of an undescribed species of *Jujubinus*, represented by 21 sps, together juveniles and fragments not included in the type series, were separated and described herein as *J. errinae* n. sp.

Additional material examined from CS-PM collection: 3 sps of *J. catenatus* from the Sicily Channel, estimated depth 90 m; about 100 sps of *J. montagui* from Anzio, Central Tyrrhenian Sea, 50 m; 9 sps from Sfax, Tunisia, 100 m; over 200 sps of *J. tumidulus* from Lampedusa Island, Sicily Channel, dredged by fishing boats, estimated depth 70–80 m; 11 sps from Linosa Island (Punta Calcarello), Sicily Channel, 36 m. Current systematics is based on WoRMS (Gofas & Bouchet, 2015).

Scanning Electron Microscopy (SEM) photographs were taken at the Interdepartmental Laboratory of Electron Microscopy (LIME, Università “Roma Tre”, Rome, Italy), using a Philips XL30.

## SYSTEMATICS

Classis GASTROPODA Cuvier, 1795  
Familia TROCHIDAE Rafinesque, 1815

Genus *Jujubinus* Monterosato, 1884

Type species (by subsequent designation of Crosse, 1885) *Trochus matoni* Payraudeau, 1826

*Jujubinus errinae* n. sp.

(Figs. 1–18, 37)

DIAGNOSIS. Small and slightly turriculate shell; sculpture of incised spiral lines; strong prosocline lamellae between spiral cords.

EXAMINED MATERIAL. The holotype (MZB60155) and paratypes A–H (DiSBA) from the type locality: Strait of Messina, (38°14'45"N 15°37'36"E), Sicily, Mediterranean Sea, dredging DG04, 100 m depth; paratypes I (DiSBA) from 38°14'45" N, 15°37'28" E, dredging DG001, St 5, 90–115 m; paratype L (DiSBA) from 38°13'27" N, 15°36'02" E, dredging PIC02, Rada Paradiso, St 2, 90–115 m; paratype M (WR) from 38°14'45" N, 15°37'28" E, dredging DG001, St 5, 90–115 m; paratype N–R (CS-PM) from 38°15'36" N, 15°43'08" E, 40–50 m depth; paratypes S–U (GN); paratype V (RM) from 38°15'36" N, 15°43'08" E, 40–50 m depth; paratype X (BA) from 38°15'36" N, 15°43'08" E, 44 m depth; paratype Y (EQ), from 38°15'36" N, 15°43'08" E, 40–50 m depth.

DESCRIPTION OF HOLOTYPE. Shell of relatively small size for the genus, height (H) 4.9 mm, width (W) 4.0 mm, conical, slightly shiny. Protoconch about 1.5 whorls, smooth, with a diameter of 280 µm. Teleoconch of 4.5 slightly convex whorls. Sculpture of 6 closely set abapical spiral cords of about the same strength, strongly carved by strong tubercles, including the 2 peripheral ones forming the basal cord, and 6 regularly spaced, basal spiral cords narrow and well engraved, with very evident lamellae in the interspaces. First two whorls of the teleoconch showing the basal cord strongly rippled, remaining teleoconch whorls with a flat basal cord. Suture incised. Teleoconch surface covered by barely visible prosocline growth striae, irregularly set. Base convex, umbilicus closed and covered with a white callus. Aperture quadrangular, with the columellar callus thickened in the middle portion and internally whitish nacreous. Colour of protoconch whitish, teleoconch reddish-creamy, with red spiral cords interrupted by short white spots. The same chromatic pattern is shown by the basal cords. Animal unknown.



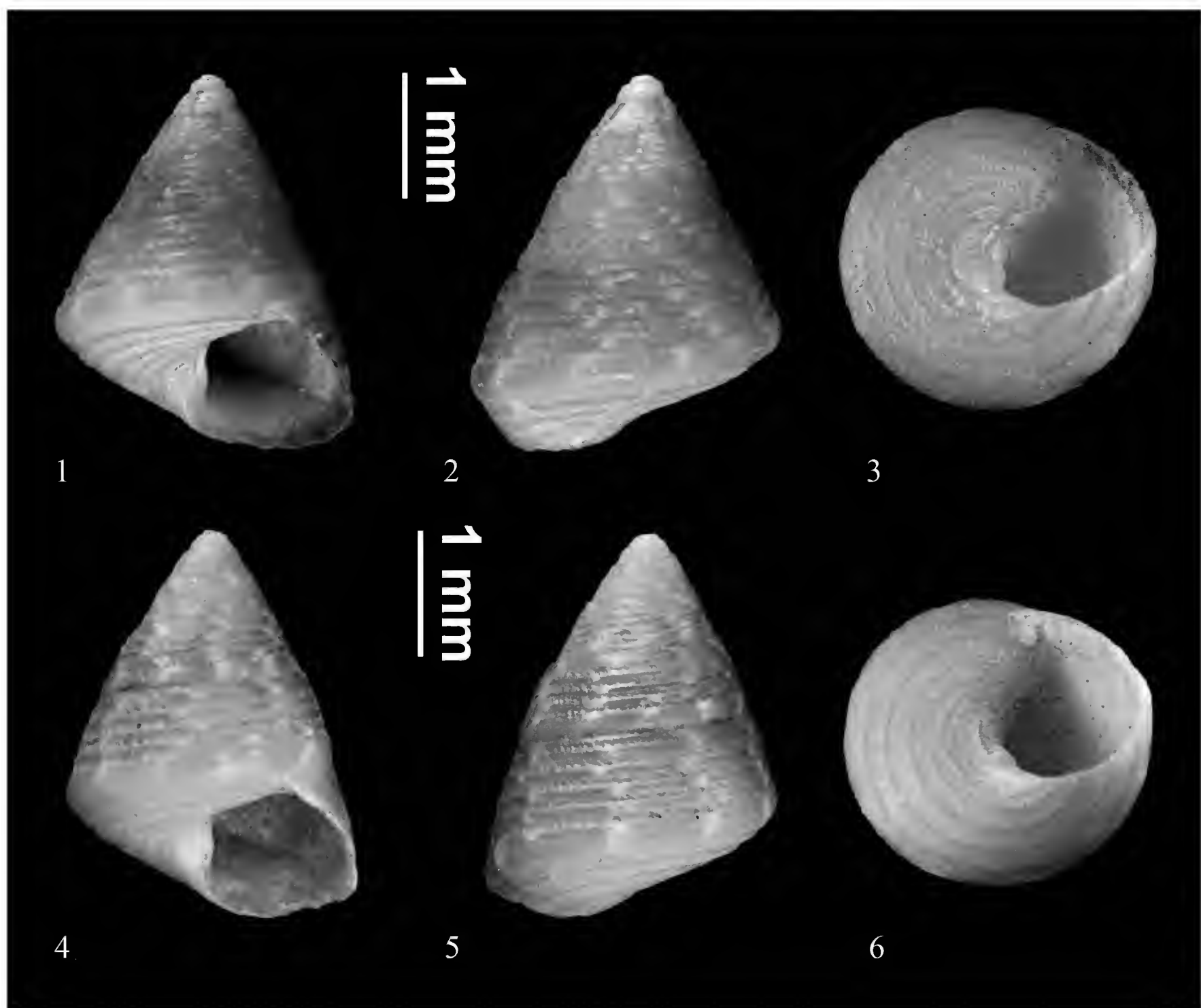
**VARIABILITY.** Shell H ranging from 4.5 to 6.0 mm and W from 3.8 to 4.7 mm. Protoconch diameter from 260 to 290  $\mu$ m. Teleoconch varying from 4 to 4.5 whorls. Spiral and basal cords both ranging from 5 to 6, according to the H of the shell (6 in adult specimens). Umbilicus is closed also in juveniles shells. Colours of protoconch, teleoconch and base very constant in all specimens observed.

**ETYMOLOGY.** The species is named after *Errina aspera* (Linnaeus, 1767) the Hydrozoan Stylasteridae whose beds characterize the type locality in Strait of Messina, Sicily.

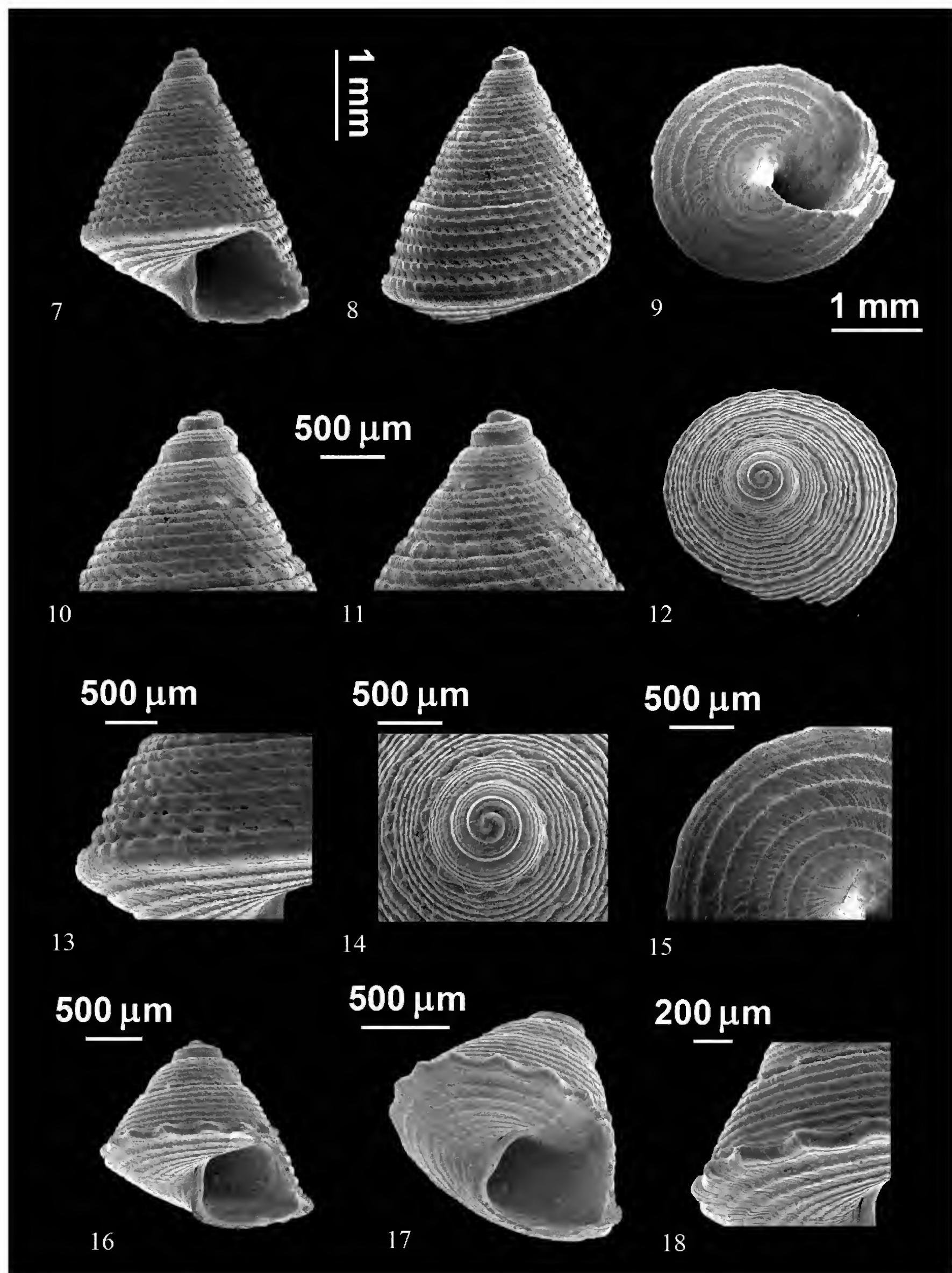
**DISTRIBUTION.** Currently only known from the type locality.

## DISCUSSION

After the institution of the genus *Jujubinus* by Monterosato (1884), in recent years an increasing number of studies have greatly contributed to a better knowledge of this group of small trochids, with the description of new species and the rediscovery of some not yet well understood ones (Bogi & Campani, 2005; Spanu, 2011; Mariottini et al., 2013; Smriglio et al., 2014; Smriglio et al., 2015). With this note we described *J. errinae* n. sp. (Figs. 1–18, 37), so increasing the number of the typical *Jujubinus* species [i.e. shell with prosocline lamellae between the spiral threads of variable strength, often beaded (Monterosato, 1884)] to be quoted for the Italian coast. The new taxon has been compared



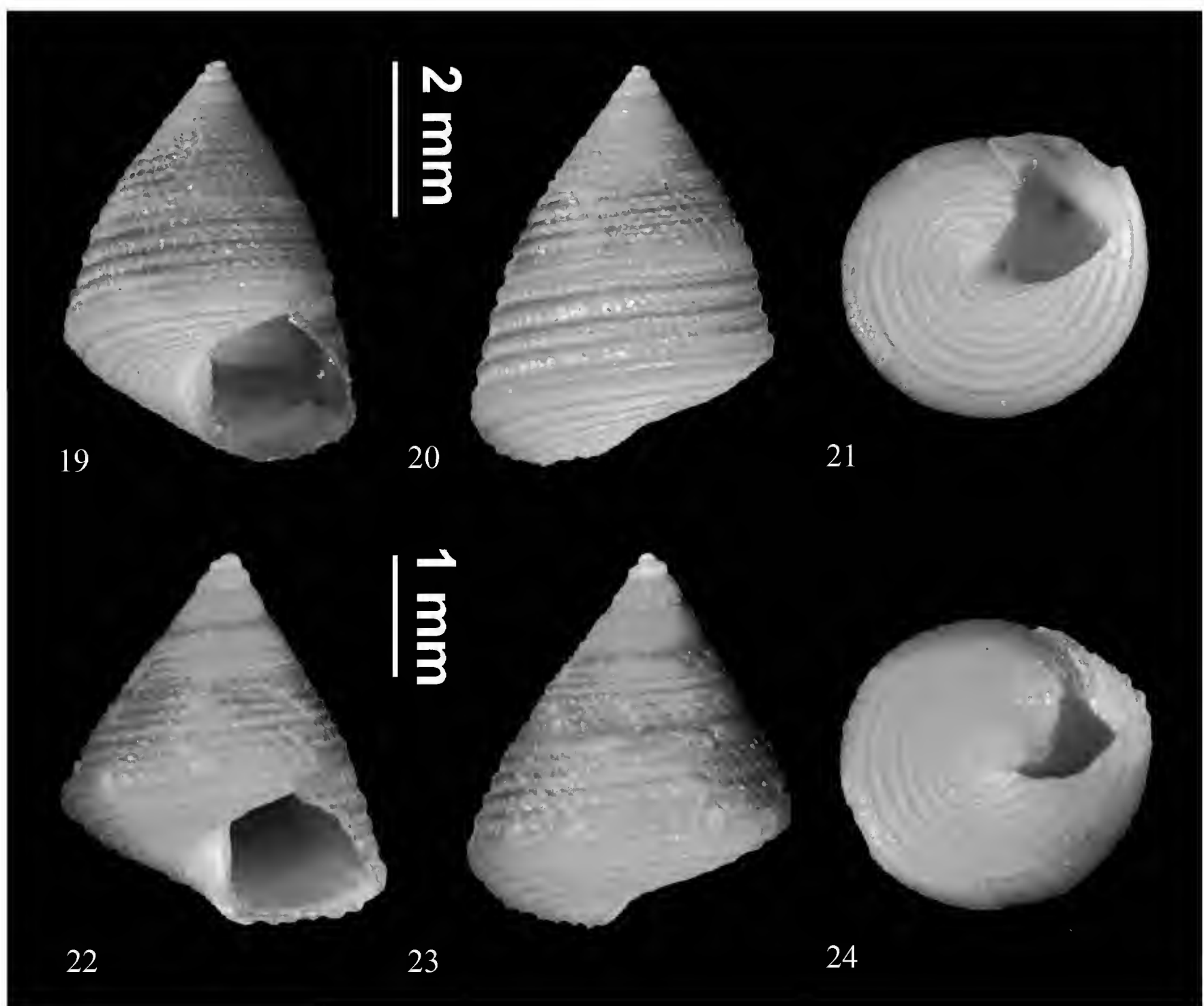
Figures 1–3. *Jujubinus errinae* n. sp., holotype (MZB60155), 4.9 mm (H) x 4.0 mm (W), from type locality (Strait of Messina), 100 m depth. Figures 4–5. *Jujubinus errinae* n. sp., paratype A (SG), 6.0 mm (H) x 4.7 mm (W) from type locality (Strait of Messina), 100 m depth.



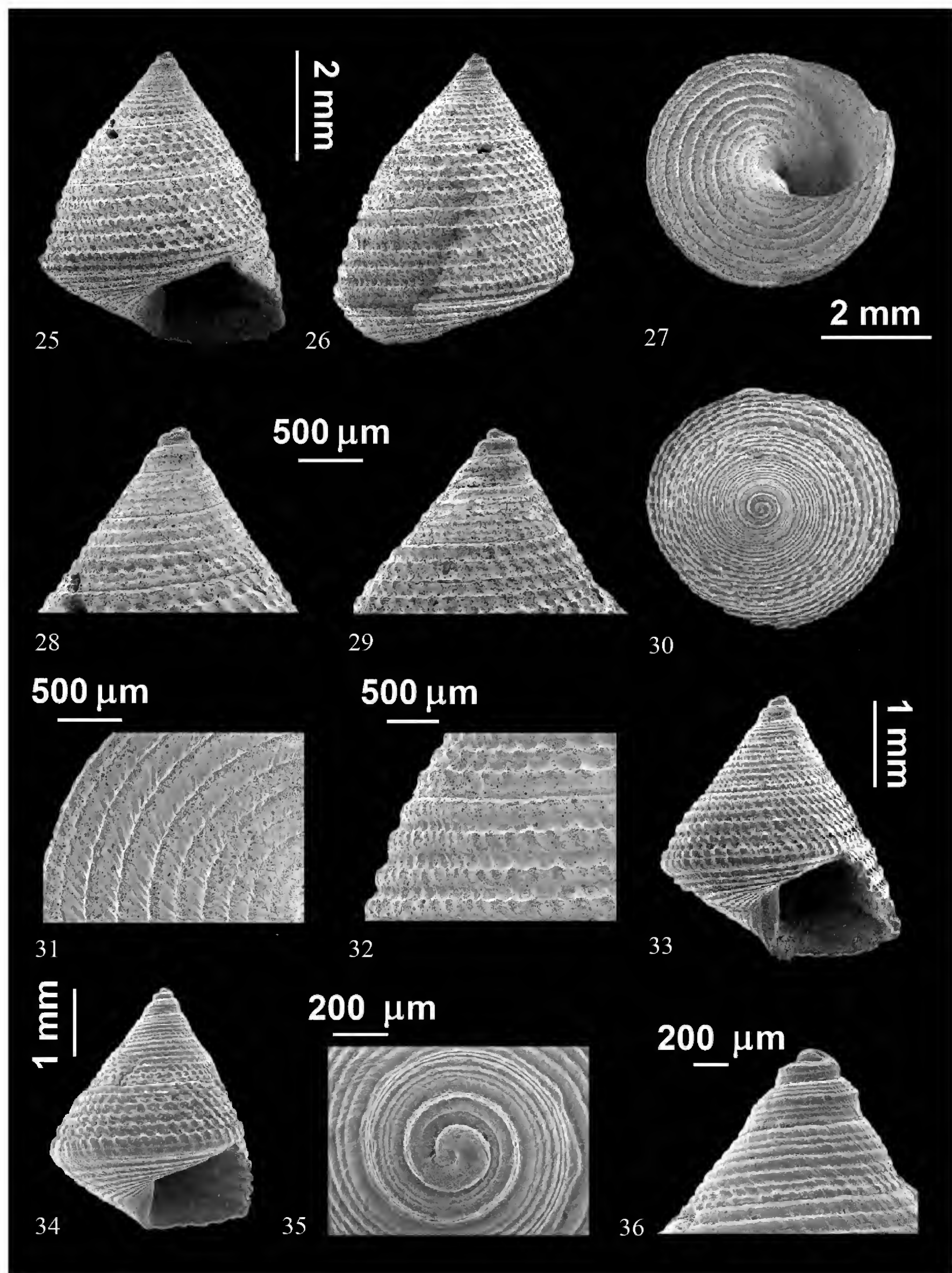
Figures 7–15. *Jujubinus errinae* n. sp., holotype, SEM analyses, details of the shell. Figures 16–18. *Jujubinus errinae* n. sp., Strait of Messina, paratype R, 1.8 mm (H) x 1.9 mm (W), CS-PM collection. Subadult specimen with basal cord sculptured by very pronounced tubercles.

with three species showing a similar sculpture and occurring in the near Sicily Channel, *J. catenatus*, *J. montagui* and *J. tumidulus* (Curini & Palazzi, 1982). In particular, *J. errinae* n. sp. differs from *J. catenatus* (Figs. 19–36), the most closely related species which has an evident “pear-shaped” shell outline and shows a stronger sculptured ornamentation of the spiral cord interspaces, as well as a different background colour, being uniformly reddish-greenish in *J. catenatus*, while the spiral cords of *J. errinae* n. sp. are white-spotted producing a typical shell pattern of irregular and interrupted axial stripes. The new species differs from *J. montagui* for its lower ratio H/W, the sculpture more tuberculate and densely ornamented with growth striae, producing a more jagged appearance of the shell surface, and the different shell chro-

matic pattern. The shell colour of *J. montagui* is generally whitish or greyish with irregular brown axial stripes and basal cords with equally spaced and alternate brown-white dashes (Scaperrotta et al., 2010). *Jujubinus errinae* n. sp. differs from *J. tumidulus* being greater in size, having a much stronger sculpture, higher ratio H/W and a different shell colour, which in the latter species is generally uniformly creamy-whitish with brown spotted spiral cords (Scaperrotta et al., 2009). Noteworthy, the new taxon shows in the initial teleoconch whorls the basal cord strongly rippled, which becomes flat in the following whorls. This morphological feature, very evident in juvenile shells (Figs. 16–18), regularly disappears during the shell development (Figs. 7–15). More generally, *J. errinae* n. sp. differs from most of the Atlantic and Mediter-



Figures 19–21. *Jujubinus catenatus* Ardochini, 2006. Sicily Channel. Figures 22–24. *Jujubinus catenatus*. Sicily Channel.



Figures 25–32. *Jujubinus catenatus* Ardovini, 2006. Specimen of figure 19. Sicily Channel, SEM analyses, details of the shell. Figure 33. *Jujubinus catenatus*. Strait of Messina, CS-PM collection. Subadult specimen. Figures 34–36. *Jujubinus catenatus*. Specimen of figure 22. Sicily Channel, SEM analyses, details of the shell.



anean *Jujubinus* species by its strongly tuberculate and jagged teleoconch sculpture, with evident lamellae in the interspaces and for its diagnostic coloration (see Description), never observed in any Recent *Jujubinus* distributed in Atlantic Ocean and Mediterranean Sea.

The new species is known currently so far only from the type locality, in the Strait of Messina, suggesting to be another new endemism for this area (Fig. 37). The Strait of Messina is a complex and diversified environment having in the tidal-induced upwelling its main physical constraint. The upwelling, causing nutrient enrichment and temperature lowering of surface water both supports exceptionally dense populations of suspension feeders (Mistri & Ceccherelli, 1995; De Domenico et al., 2009) and allows the settlement of Pliocene Atlantic remnants (Fredj & Giaccone, 1995). In this area, hard substrate corresponding to the Colantoni et al. (1981) “rough bottoms with pinnacles”, are characterized by dense and extensive colonies of the Hydrozoan Stylasteridae *Errina aspera*, known only for Gibraltar and the Messina Straits, which hosts an abundant and peculiar benthic fauna of Atlantic origin (Giacobbe & Spanò, 2001; Giacobbe et al., 2007). Such well-known associated fauna was found in the sampled *E. aspera* beds (DG001 and DG04; 90–115 m depth), together with less frequent “accessory” species, as the bivalve *Spondylus gussoni* O.G. Costa, 1829, and the here described *J. errinae* n. sp. Such associated fauna was also found deeper (St 02; 201 m depth), on partially consolidated coarse sediment, colonized by *E. aspera* together with the giant barnacle

*Pachylasma giganteum* (Philippi, 1836). Differently, the bathyal bottom sediment collected on the Gioia Basin slope (St 1B; 371 m), characterized by terrigenous gravelly sands, showed a mixture of autochthonous (bathyal) and allochthonous (subtidal) bioclastic remains, which included *J. errinae* n. sp. specimens. Interestingly, in the same geographical area is present *Jujubinus curinii* Bogi et Campani, 2005, another endemism belonging to the so-called “smooth” *Jujubinus* complex (Smriglio et al., 2014 and references therein). Such co-occurrence of congeneric endemisms is not surprising, since the two species are living in different habitats whose peculiarities have been put in evidence in literature. *Jujubinus errinae* n.sp., as accessory species in the *E. aspera* assemblages, might represent a further Atlantic relict fauna having in the Strait of Messina its areal distribution.

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Figure 37. Distribution of *Jujubinus errinae* n. sp.



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# Check-list of the Nudibranchs (Mollusca Gastropoda) from the biodiversity hot spot “Scoglio del Corallo” (Argentario promontory, Tuscany)

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## ABSTRACT

The Mediterranean nudibranch (Mollusca Gastropoda) fauna is part of complex communities belonging to the Mediterranean endemic “Coralligenous”. This important ecosystem shows a high species richness and functional diversity with assemblages of species tied together by major trophic and ecological relationships. A first check-list for the biodiversity hot spot “Scoglio del Corallo”, located along the coast of the Argentario promontory (Tuscany, Tyrrhenian Sea) is here reported.

## KEY WORDS

Nudibranchs; biodiversity; check-list; Tyrrhenian Sea.

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## INTRODUCTION

Nudibranchs are molluscs brightly coloured and frequently photographed by Scuba diver amateurs, since these sea slugs can be found in most coastal areas of the world, from polar to tropical waters. The most Nudibranchia diversity is known for shallow waters, ranging 0–30 m depth, but deep-sea research is unravelling high levels of previously unknown diversity of these molluscs at high depths too (Valdés, 2008; Oskars et al., 2015). The Mediterranean nudibranch diversity to date is of about 270 species, according to more recent checklists (Öztürk et al., 2014; Trainito & Doneddu, 2014), regional faunal catalogues and Internet forum (WoRMS, Sea-slug forum). Although Mediterranean nudibranch species richness is smaller than that of the Indo-Pacific biogeographic region or the Caribbean Sea (Atlantic Ocean), the Mediterranean fauna has a high level of endemic diversity. Their scarce

mobility in some cases leads them to live their entire life cycle associated to their trophic source and this is the reason why they are deeply related to the most important endemic habitats of the semi-closed Mediterranean Sea. In fact, they are common inhabitants of the Mediterranean benthic ecosystem defined as “Coralligenous” (Ballesteros, 2006), where they livefeeding on a broad range of different substrates (Sponges, Cnidarians, Bryozoans, Tunicates and other sessile animals) (Gutiérrez, 2015). These complex communities are composed of a wide variety of suspension feeders, exhibiting high species richness and functional diversity (Gili & Coma, 1998). Recent molecular studies (e.g., Schrödl et al., 2011; Zapata et al., 2014) have proposed a new classification on the base of the polyphyly showed by this group that nowadays is split into 3 different Suborders (WoRMS: Gofas, 2015). This work aims to produce the first comprehensive catalogue of the nudibranchs for the Biod-

iversity hot spot “Scoglio del Corallo”, located along the coast of the Argentario Promontory (Tuscany, Tyrrhenian Sea) (Figs. 1–3), based on a fieldwork carried out by the authors in the last two years. An annotated Nudibranch checklist is produced discussing taxonomic problems and new ecological data (association with other organisms, parasitism, cryptic species and geographical distribution) whenever relevant. Each species observed has been photographed in field and ecological and distribution data are provided for all species recorded.

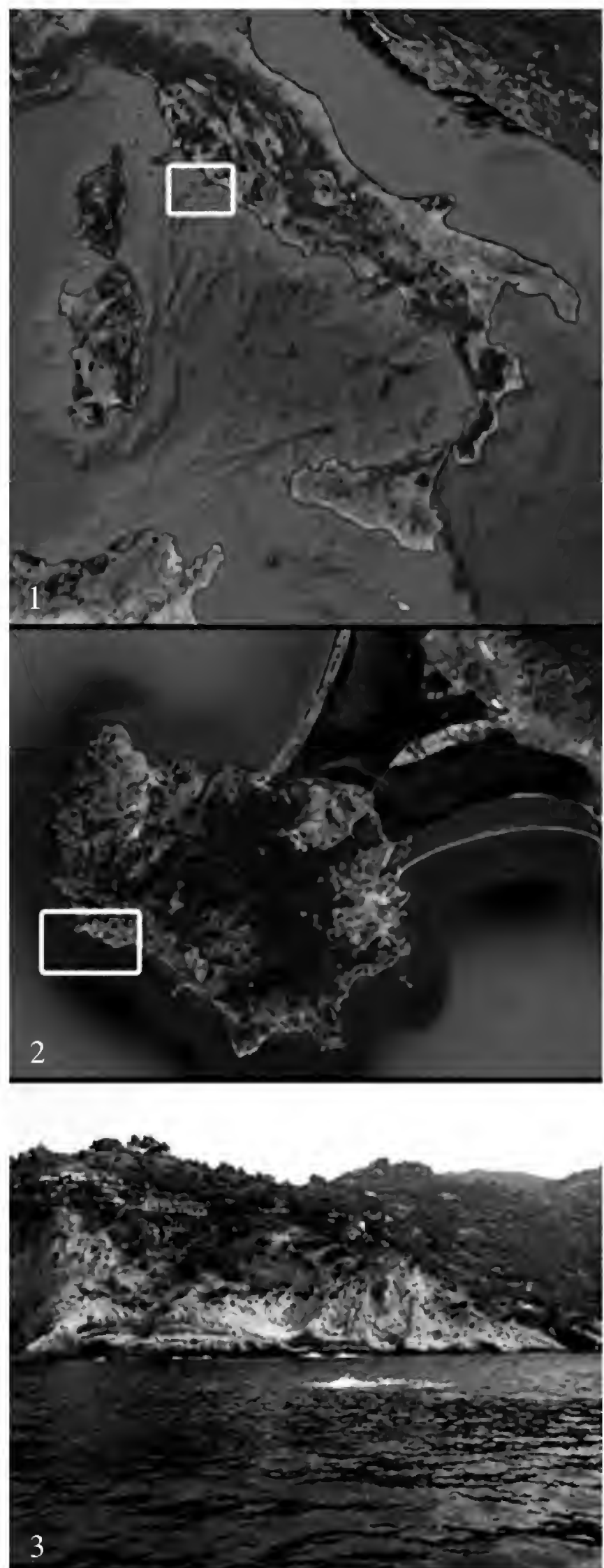
## MATERIAL AND METHODS

### *Sampling area*

“Scoglio del Corallo” is an underwater rocky habitat located in the in National Park of “Arcipelago Toscano” ( $42^{\circ}23'60.00''\text{N}$ ,  $11^{\circ}5'30.00''\text{E}$ , Central Tyrrhenian Sea). This submarine formation outcrops just for a few centimetres (depending on the marine tide) from the surface and slopes down vertically to a depth of 35 meters (Figs. 3, 4). The most relevant inhabitant of this area is the Octocoral *Corallium rubrum* (Linnaeus, 1758) (Cnidarian), a Mediterranean endemic species included in several European and International protocols for conservation, like the FAO General Fisheries Commission for the Mediterranean (GFCM) and the Convention on International Trade in Endangered Species (CITES). The presence of *C. rubrum* seems to be closely related to the high level of biodiversity characteristic of this area (Gili & Coma, 1998) (Figs. 5–9). This site is very small in extent (about  $500\text{ m}^2$ ), but nevertheless characterized by a set of rocks and walls forming canyons, caves and platforms placed on a muddy substrate creating a lot of microhabitats where a conspicuous number of species live and reproduce (Fig. 5).

### *Protocol Sampling*

Sampling took place between the years 2013 to 2015 as a part of a broader research project (“Project Baseline *Corallium rubrum*”, directed by the “Global Underwater Explorer” No-Profit Organization) aiming to produce the first characterization of this biota and of its associated biocoenoses. The produced preliminary data will become the starting



Figures 1–3. Study area. Location of the “Scoglio del Corallo” (“Arcipelago Toscano”,  $42^{\circ}23'60.00''\text{N}$ ,  $11^{\circ}5'30.00''\text{E}$ , Central Tyrrhenian Sea) in the Mediterranean Sea.

point for monitoring future environmental changes and to evaluate possible conservation strategies. Materials were sampled using SCUBA diving techniques. Specimens were obtained by manual collecting, photographed and fixed for future DNA extraction and anatomical studies in 96 % ethanol. Some species were observed and photographed on their natural habitat during field campaigns, but not captured.

## RESULTS AND DISCUSSION

For the first time a Nudibranchs catalogue from a Tyrrhenian Sea submarine hot spot of biodiversity is here provided. A total of 23 species of nudibranchs belonging to 9 different families were collected during the project. Among these, 4 are endemics of the Mediterranean Sea showing the importance of this Mediterranean coralligenous assemblage. All collected species coexist in this small area according to the high biodiversity showed by this hot spot marine site. The list of the sampled species is here reported, with notes on their ecology and distribution according to OPK-Opisthobranchis (Available from <http://opisthobranchis.info/en/>), Sea Slug Forum (Australian Museum, Sydney, Available from <http://www.seaslugforum.net/>), World Register of Marine Species (WoRMS, Available from <http://www.marinespecies.org> at VLIZ), “Sea slug of the Algarve” (Calado & Silva, 2012), “Nudibranchi del Mediterraneo” (Trainito & Doneddu, 2014) and personal underwater observations.

Phylum MOLLUSCA  
Classis GASTROPODA  
Subclass HETEROBRANCHIA  
Infraclass OPISTHOBRANCHIA  
Order NUDIBRANCHIA  
Suborder DEXIARCHIA  
Infraorder CLADOBRANCHIA  
Parvorder AEOLIDIDA

Familia FACELINIDAE Bergh, 1889  
Genus *Cratena* Bergh, 1864

### 1. *Cratena peregrina* (Gmelin, 1791) (Fig. 10)

ECOLOGY. This species commonly feeds on hydroids of the genus *Eudendrium* Ehrenberg, 1834

on which it usually lays eggs. *Cratena peregrina* lives between a few meters from the surface till about 50 meters depth.

DISTRIBUTION. It has been found from Western to Eastern basin of the Mediterranean Sea, in the Portuguese and Andalusian Atlantic coasts and in the Canary Islands. It was also informally recorded from Senegal, South Africa, India and in Western Atlantic.

Genus *Facelina* Alder et Hancock, 1855

### 2. *Facelina annulicornis* (Chamisso et Eysenhardt, 1821) (Fig. 11)

ECOLOGY. This species has a varied diet consisting on different genera of Hydrozoans: *Eudendrium* Ehrenberg, 1834, *Obelia* Péron et Lesueur, 1810, *Pennaria* Goldfuss, 1820 and *Tubularia* Linnaeus, 1758.

DISTRIBUTION. WoRMS (2015) recorded it from Mediterranean Sea and Atlantic Ocean (Ireland, United Kingdom, Azores, Portugal). The recent work of Öztürk et al. (2014) expands its distribution range to the Turkish coasts of Aegean Sea.

### 3. *Facelina rubrovittata* (Costa A., 1866) (Fig. 12)

ECOLOGY. The few pictures of this rare nudibranch often show it staying on algae substratum. On the diet of *F. rubrovittata* little is known but it seems to feed on hydrozoans as well as most of the aeolids do.

DISTRIBUTION. It is distributed from the whole Mediterranean Sea till the Atlantic coasts of Spain.

Familia FLABELLINIDAE Bergh, 1889  
Genus *Calmella* Eliot, 1910

### 4. *Calmella cavolini* (Vérany, 1846) (Figs. 13, 14)

ECOLOGY. This aeolid species usually feeds on *Halecium pusillum* Sars, 1856 and *Eudendrium racemosum* (Cavolini, 1785) but can be found on different substrates. This small nudibranch can be easily misidentified with the sibling species *Piseinotecus gaditanus* Cervera, García-Gómez et García, 1987 from which it can be recognized by the absence, on its cerata, of the little white spots typical of *P. gaditanus*. Interestingly we could observe some individuals (Fig. 14) with very few

white dots, whose identification needs possibly a DNA barcoding approach.

**DISTRIBUTION.** This endemic species originally was found only in the western coast of Mediterranean Sea but on the base of recent records its distribution range now includes also the Turkish coasts and the Atlantic coast of the Iberian Peninsula.

Genus *Flabellina* Gray, 1833

**5. *Flabellina affinis*** (Gmelin, 1791) (Fig. 15)

**ECOLOGY.** *Flabellina affinis* is a very common species present all year long often feeding on colonies of *Eudendrium* spp. and belongs to the complex of the ‘pink Flabellinidae species’, see below *F. ischitana* and *F. pedata*. This species usually co-exists in the same arborescent hydrozoan colony with *C. peregrina* and can be parasitized by Copepods of the family Splanchnotrophidae, whose eggs often can be seen extruding from the notum of the host.

**DISTRIBUTION.** This is one of the most common European species ranging it from the eastern coast of Mediterranean Sea to the Atlantic basin of Spain and Portugal and in the Canarias islands.

**6 *Flabellina babai*** Schmekel, 1972 (Fig. 16)

**ECOLOGY.** This species shows a large body size atypical for a common ‘Flabellinid’. It can be found easily on different substrates mostly on hydroids of the genus *Campanularia* Lamarck, 1816, *Eudendrium* Ehrenberg, 1834 and *Bougainvillea* Lesson, 1830, but is still unclear if it feeds on them.

**DISTRIBUTION.** This species has been recorded throughout the Mediterranean Sea and also in Senegal.

**7. *Flabellina ischitana*** Hirano et Thompson, 1990 (Fig. 17)

**ECOLOGY.** This species feeds on two different species of athecate hydrozoans of the genus *Eudendrium*, i.e. *E. racemosum* (Cavolini, 1785) and *E. glomeratum* Picard, 1952 often coexisting with *F. affinis*. They are morphologically very similar and easily confused with each other and, as mentioned above, both belong to the complex of the ‘pink Flabellinidae species’.

**DISTRIBUTION.** Its distribution overlap with the geographical range of *F. affinis* going from eastern basin of Mediterranean sea to the Atlantic coast of Iberian peninsula.

**8. *Flabellina lineata*** (Lovén, 1846) (Fig. 18)

**ECOLOGY.** Mediterranean specimens of this ‘Flabellinid’ usually feed on *Eudendrium* spp. while the extra-Mediterranean individuals were observed on different species of hydroids like *Tubularia indivisa* Linnaeus, 1758, *Coryne eximia* Allman, 1859, *Hydrallmania falcata* (Linnaeus, 1758) and *Sertularia argentea* Linnaeus, 1758.

**DISTRIBUTION.** This species is distributed in the Atlantic Ocean, from the Arctic Circle to the French Atlantic coast, and in the European waters.

**9. *Flabellina pedata*** (Montagu, 1816) (Fig. 19)

**ECOLOGY.** *Flabellina pedata* also belongs to the complex of the ‘pink Flabellinidae species’, see above, being very similar to *F. affinis* and *F. ischitana* from which differs on the base of possessing single cerata, not clustered together on a single peduncles, and by a smoothed rhinophores. It feeds on athecate hydrozoans of genus *Eudendrium* (especially in the Mediterranean Sea), but also on sertularids of genus *Abietinaria* Kirchenpauer, 1884 and on the plumularid genus *Aglaophenia* Lamouroux, 1812. Recently was discover a new species of Flabellinid, *Flabellina albomaculata* Pola, Carmona, Calado et Cervera, 2014, very similar to *F. pedata* and easily confused with it.

**DISTRIBUTION.** This common Flabellinid is distributed from eastern basin of the Mediterranean Sea to the Strait of Gibraltar and in the Atlantic Ocean from the Azores to the North Atlantic Coast of Norway.

Parvorder CLADOBRANCHIA

Familia PROCTONOTIDAE Gray, 1853

Genus *Janolus* Bergh, 1884

**10. *Janolus cristatus*** (Delle Chiaje, 1841) (Fig. 20)

**ECOLOGY.** This species lives between 10 and 40 m deep on a rocky substrate. Usually it was associated to different Bryozoans on which *J. cristatus* seemed to feed on. *Alcyonidium gelatinosum* (Hud-



son) J.V. Lamouroux, *Bicellariella ciliata* (Linnaeus, 1758), *Bugulina avicularia* (Linnaeus, 1758), *B. flabellata* (Thompson in Gray, 1848), *B. turbinata* (Alder, 1857), *Bugula neritina* (Linnaeus, 1758) and species of genus *Cellaria* Ellis et Solander, 1786 were cited as a presumed preys.

DISTRIBUTION. It is commonly found throughout the Mediterranean Sea and in the North-eastern Atlantic Ocean from Norway to Morocco coasts.

Parvorder DENDRONOTIDA

Familia TRITONIIDAE Lamarck, 1809

Genus *Marionia* Vayssière, 1877

11. *Marionia blainvillea* (Risso, 1818) (Fig. 21)

ECOLOGY. It is recorded to feed on different preys like *Alcyonium acaule* Marion, 1878, *A. palmatum* Pallas, 1766, *Eunicella cavolinii* (Koch, 1887), *E. singularis* (Esper, 1791), *Eunicella* sp., *Leptogorgia sarmentosa* (Esper, 1789), *Paramuricea clavata* (Risso, 1826). The juveniles have different body colours; in particular they are completely white while the adults range in colour from a pale translucent orange to a deeper reddish brown with irregular white patches. They can be parasitized by Copepods like the ectoparasitic *Doridicola comai* Conradi, Megina et López-González, 2004 and the endoparasitic *Linaresia bouligandi* Stock, 1979 and *L. mammillifera* Zulueta, 1908.

DISTRIBUTION. Its geographical range goes from the whole Mediterranean Sea to the North-eastern and South-eastern Atlantic Ocean (Angola).

Genus *Tritonia* Cuvier, 1798

12. *Tritonia manicata* Deshayes, 1853 (Fig. 22)

ECOLOGY. This species lives in shallow and very bright waters between the rhizomes of *Posidonia oceanica* (Linnaeus) Delile, 1813 or on a rocky substrates where it can find a lot of Anthozoan (Cnidaria) species. The *Stoloniferous* group is the one on which *T. manicata* seems to feed on, in particular on genus *Cornularia* Lamarck, 1816 and *Clavularia* Greville, 1865.

DISTRIBUTION. Present along the coasts of the Mediterranean Sea and also recorded from coast of Morocco and North-Atlantic British islands.

13. *Tritonia striata* Haefelfinger, 1963 (Fig. 23)

ECOLOGY. This species lives in shallow waters on rocky substrates full of algae, sponges and cnidarians. It has been recorded to feed on the soft coral *Paralcyoniums pinulosum* Delle Chiaje, 1822.

DISTRIBUTION. *Tritonia striata* is known to be endemic of the Mediterranean Sea but recently it has been also recorded from the Gulf of Biscay in North Atlantic Ocean.

Suborder EUCTENIDIACEA

Infraorder DORIDACEA

Familia ONCHIDORIDIDAE Gray, 1827

Genus *Diaphorodoris* Iredale et O'Donoghue, 1923

14. *Diaphorodoris papillata* Portmann et Sandmeier, 1960 (Fig. 24)

ECOLOGY. It feeds on Bryozoans so it is often observed in habitats rich in algae and sessile invertebrate fauna.

DISTRIBUTION. This species is endemic of the Mediterranean Sea but recorded also from coasts of Portugal and Strait of Gibraltar.

15. *Diaphorodoris luteocincta* var. *alba* (M. Sars, 1870) (Fig. 25)

ECOLOGY. It is reported to feed on different bryozoans genus *Smittina* Norman, 1903, *Cellepora* Linnaeus, 1767 and *Crisia* Lamouroux, 1812. It can be found in a rock walls hosting bryozoans, scyaphilic algae, hydroids and sponges.

DISTRIBUTION. There are two different morphotypes referring to *D. luteocincta* var. *alba* and *D. luteocincta* var. *reticulata* on the base of a dorsal notum completely white (var. *alba*) or red coloured (var. *reticulata*). These two morpho variants share the same wide distribution inhabiting the Mediterranean Sea and North-Eastern Atlantic Ocean (Trainito & Doneddu, 2014).

Familia POLYCERIDAE Alder et Hancock, 1845

Genus *Polycera* Cuvier, 1816

16. *Polycera quadrilineata* (O. F. Müller, 1776) (Fig. 26)

ECOLOGY. Different species of Bryozoans were reported to be the substrate (possibly food) of the

*P. quadrilineata*. This species lives in a rocky habitats where is relatively common. This species is often parasitized by Copepod Crustaceans belonging to the genus *Splanchnotrophus* Hancock et Norman, 1863 with the injection of its eggs into the body tissues of its host.

DISTRIBUTION. This species is distributed in Western Europe from Iceland and Greenland to the entire Mediterranean Sea.

Familia CHROMODORIDIDAE Bergh, 1891  
Genus *Felimare* Ev. Marcus et Er. Marcus, 1967

17. *Felimare fontandraui* (Pruvot-Fol, 1951) (Fig. 27)

ECOLOGY. *Felimare fontandraui* feeds on Sponges belonging to the genus *Dysidea* Johnston, 1842. This species can be found during all the year from the intertidal zone to about forty meters deep. It is very variable in colour morphs and some specimens can be misidentified with the sister species *Felimare tricolor* (Cantraine, 1835) from which can be recognized by the presents of a white basal spots on the rhinophores and other diagnostic characters.

DISTRIBUTION. Its distribution ranges from both the eastern and western Mediterranean basins to the North-eastern Atlantic coasts.

18. *Felimare picta* (Schultz in Philippi, 1836) (Fig. 28)

ECOLOGY. This species feeds on different sponges like species belonging to genus *Ircinia* Nardo, 1833, *Crella* Gray, 1867 and *Dysidea* Johnston, 1842. This common species lives on rocky substrate and shows different colour morphotypes described in the past like different subspecies.

DISTRIBUTION. *Felimare picta* has a wide spread distribution. It lives from the western coast of the Atlantic Ocean, Brazil and Florida, to the eastern Atlantic, Spanish and African coast as well and in the entire Mediterranean Sea.

19. *Felimare tricolor* (Cantraine, 1835) (Fig. 29)

ECOLOGY. *Felimare tricolor* lives in rocky substrates from intertidal zone to about hundred meters deep. It feeds on different genera of sponges; *Dysidea* Johnston, 1842, *Scalarispongia* Cook et Bergquist, 2000 and *Spongia* Linnaeus, 1759.

DISTRIBUTION. This common species is distributed in the Mediterranean Sea and in the North-eastern Atlantic Ocean.

Genus *Felimida* Ev. Marcus, 1971

20 *Felimida krohni* (Vérany, 1846) (Fig. 30)

ECOLOGY. This species has a morphology similar to the sister species *Felimida britoi* (Ortea & Pérez, 1983), from which can be recognized by differences in the shape of the rhinophores and the mantle colour pattern. Its bathymetric range goes from subtidal zone down to 50 meters depth where it lives on different sponges like *Hymeniacidon perlevis* (Montagu, 1814) and species of genus *Ircinia* Nardo, 1833. Its diet is still not clear.

DISTRIBUTION. The distribution of this species goes from the eastern basin of the Mediterranean Sea to the Strait of Gibraltar. It lives also in the North eastern Atlantic Ocean from Canary Islands and north coasts of Africa to the Atlantic coasts of Spain and France.

21. *Felimida luteorosea* (Rapp, 1827) (Fig. 31)

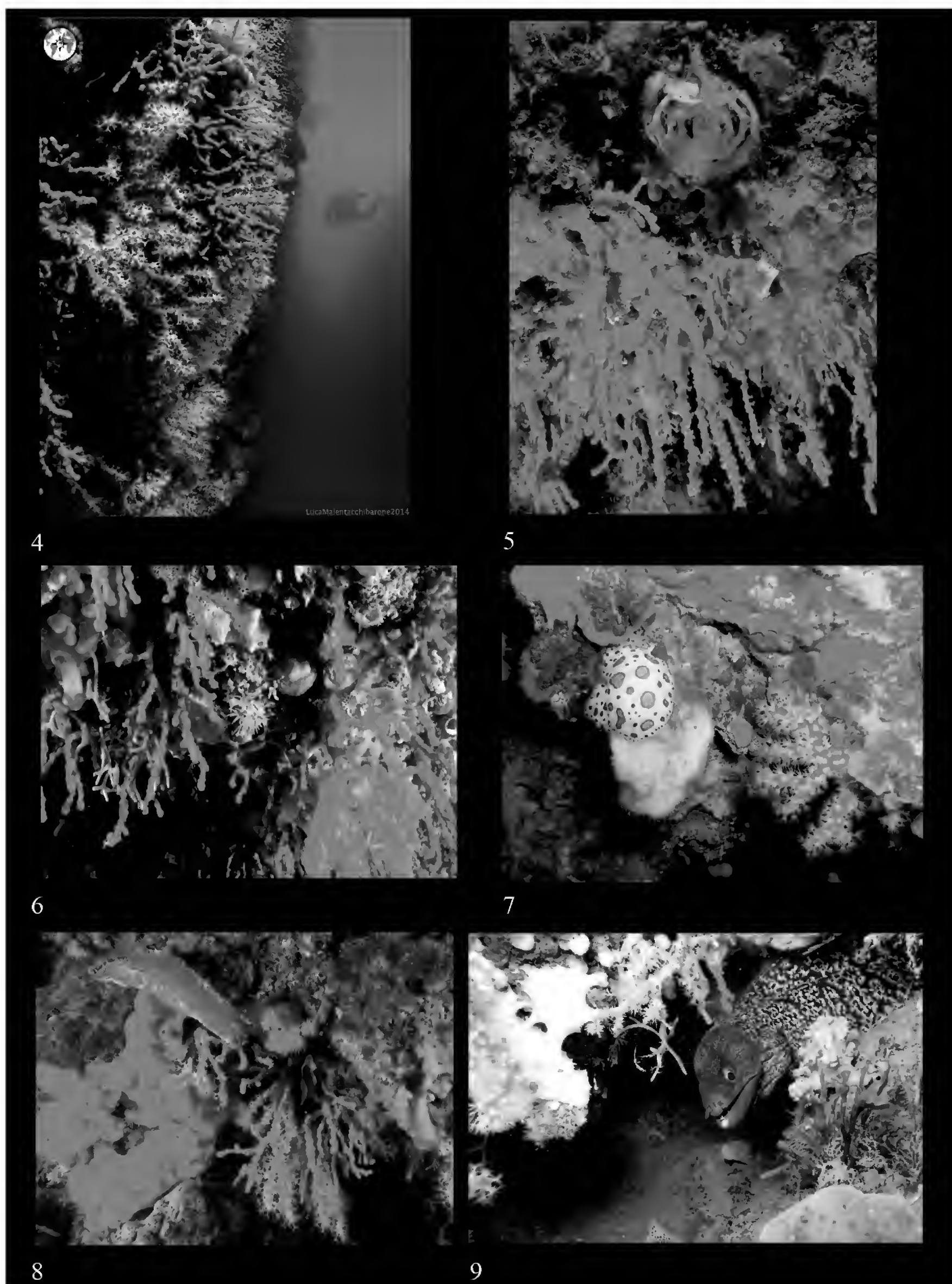
ECOLOGY. It lives under stones and on illuminated precoralligenous walls from 10 to 50 meters deep. It is reported to feeds on sponges like *Aplysilla rosea* (Barrois, 1876) and *Spongionella pulchella* (Sowerby, 1804).

DISTRIBUTION. It is distributed in the Mediterranean Sea and in the North Atlantic Ocean from the north coast of France and Spain to Angola and Canary islands.

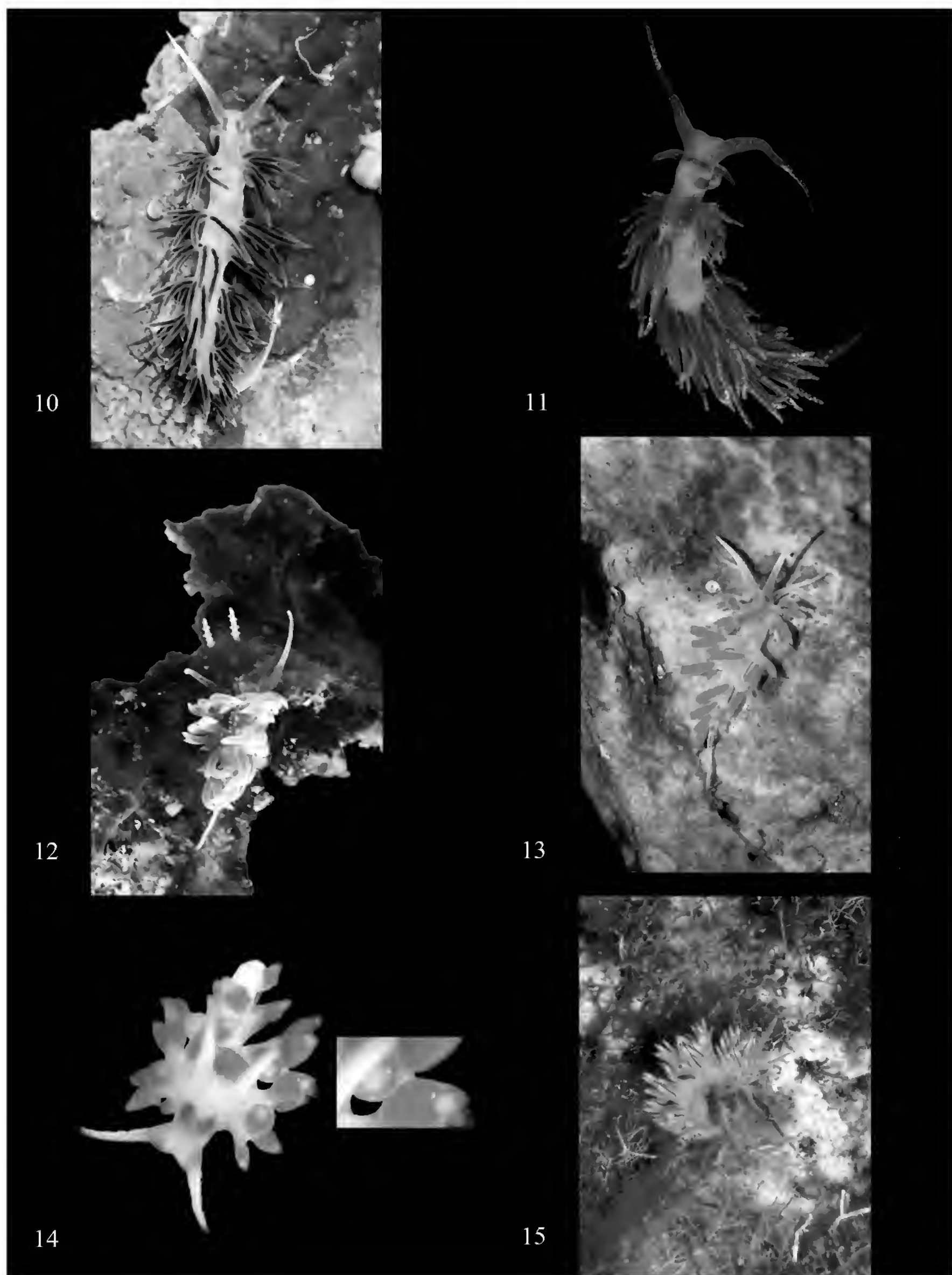
Familia DISCODORIDAE Bergh, 1891  
Genus *Peltodoris* Bergh, 1880

22. *Peltodoris atromaculata* Bergh, 1880 (Fig. 32)

ECOLOGY. This common nudibranch lives on rocky bottoms usually associated to its prey, the sponge *Petrosia* (*Petrosia*) *ficiformis* (Poiret, 1789). It is extremely abundant in the coralligenous where it lives searching for its food or staying on it. This sea slug is very sedentary so it can be found on the same sponge for different days.

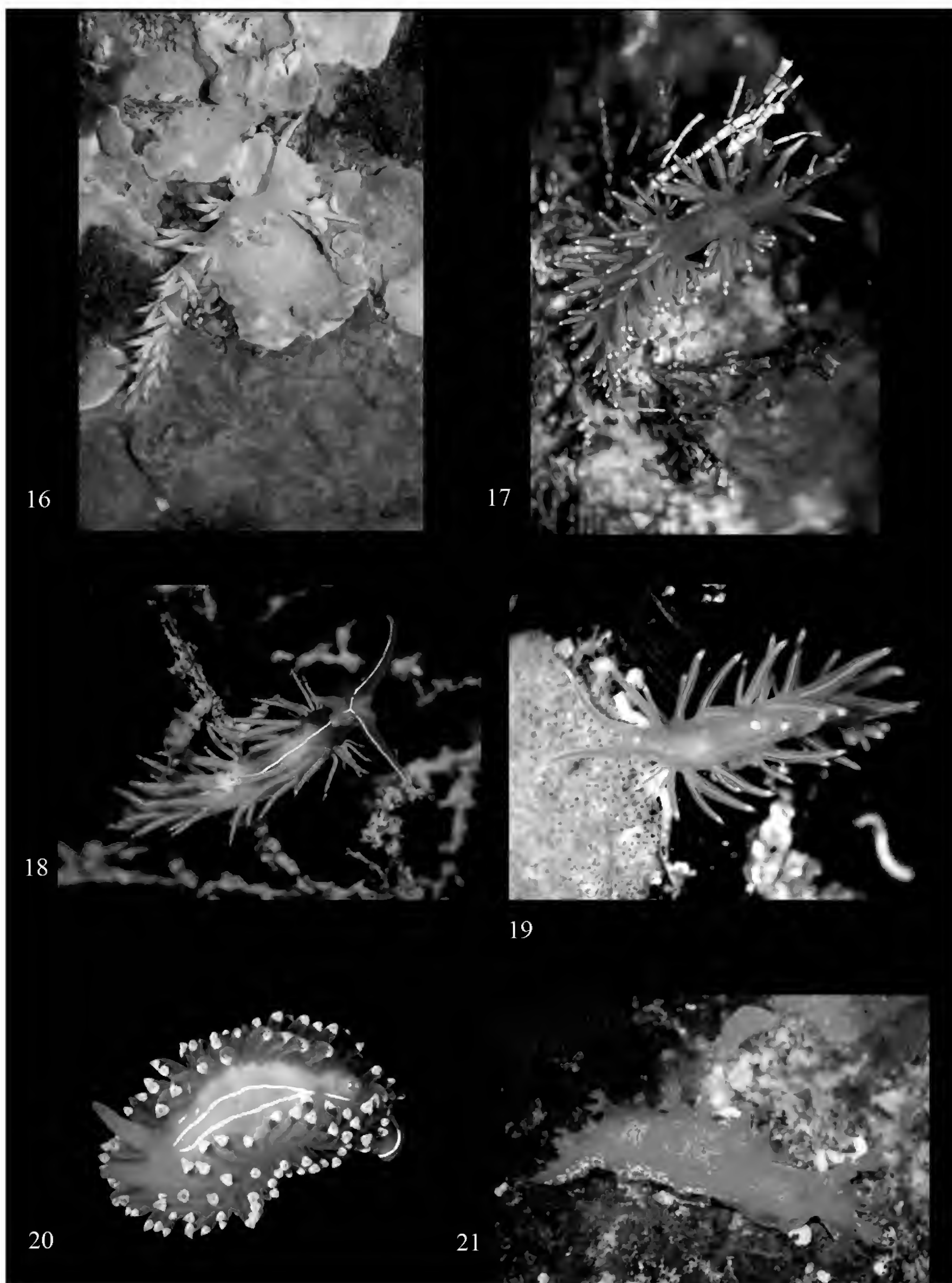


Figures 4–9. Underwater photographs of the “Scoglio del Corallo”, showing the *Corallium rubrum* assemblages.



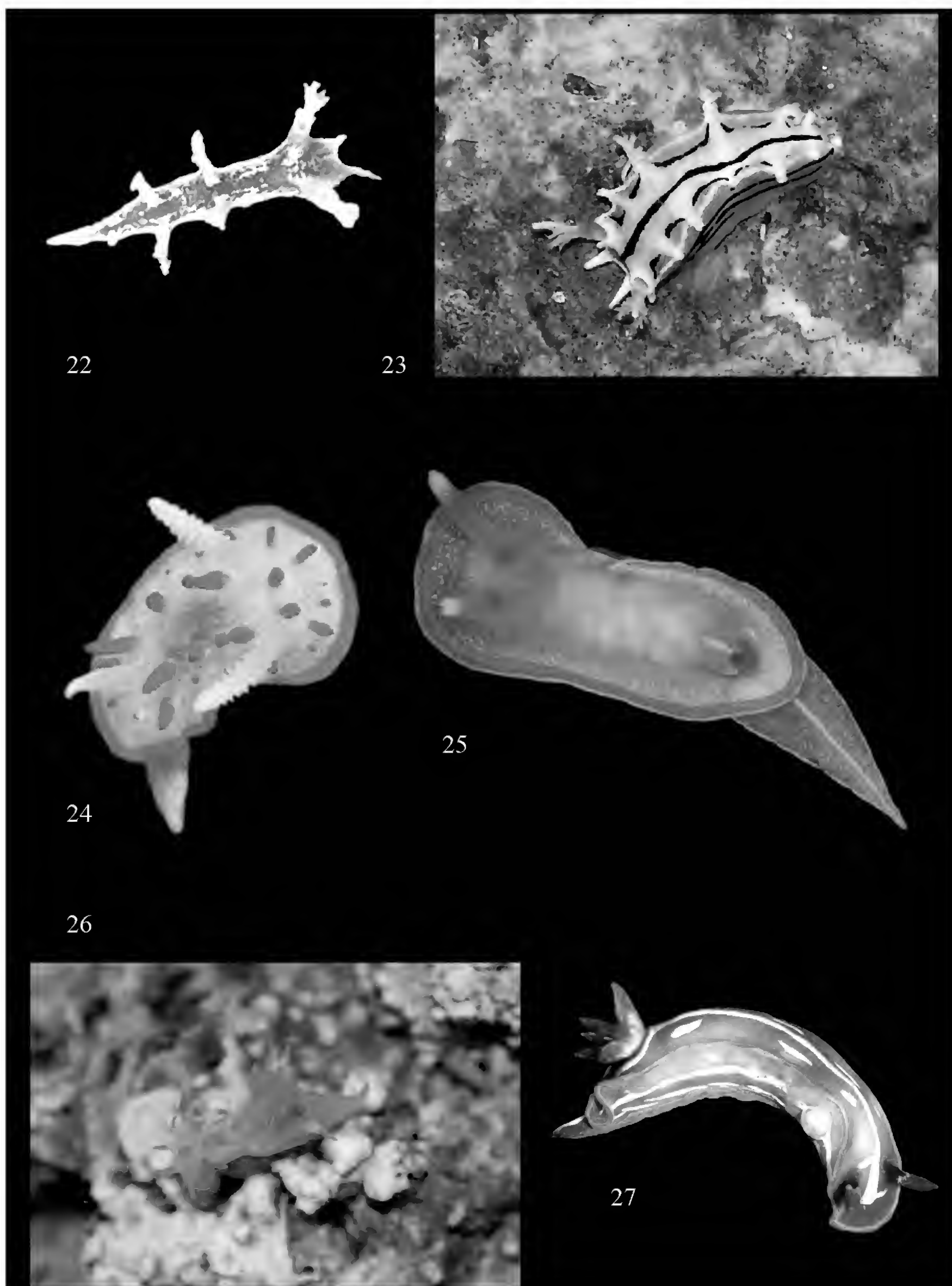
Figures 10–15. Fig. 10: *Cratena peregrina* (Gmelin, 1791). Fig. 11: *Facelina annulicornis* (Chamisso et Eysenhardt, 1821). Fig. 12: *Facelina rubrovittata* (Costa A., 1866). Figs. 13,14: *Calmella cavolini* (Vérany, 1846). Fig. 15: *Flabellina affinis* (Gmelin, 1791).



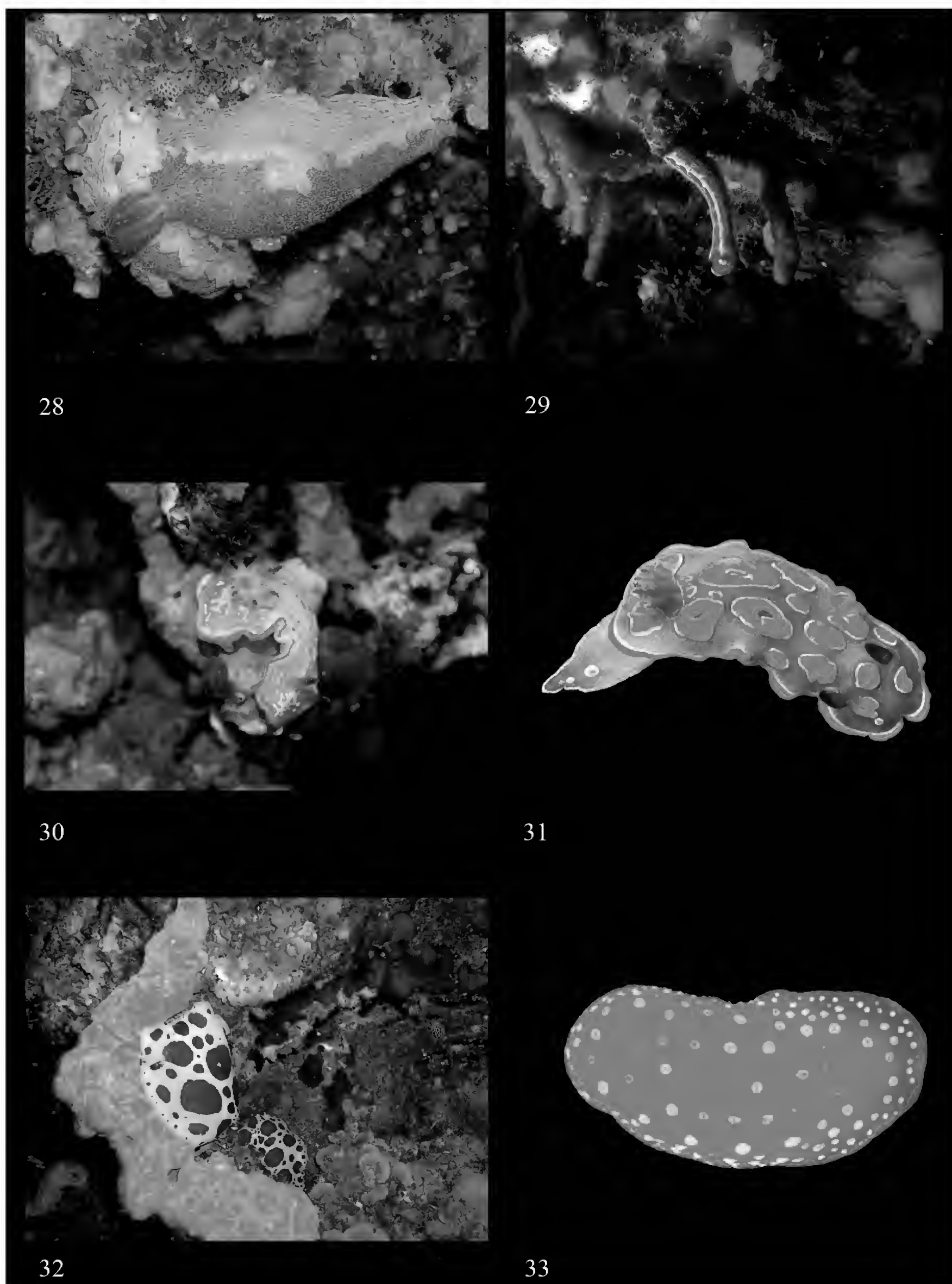


Figures 16–21. Fig. 16: *Flabellina babai* Schmekel, 1972. Fig. 17. *Flabellina ischitana* Hirano et Thompson, 1990. Fig. 18. *Flabellina lineata* (Lovén, 1846). Fig. 19: *Flabellina pedata* (Montagu, 1816). Fig. 20: *Janulus cristatus* (Delle Chiaje, 1841). Fig. 21: *Marionia blainvillea* (Risso, 1818).





Figures 22–27. Fig. 22: *Tritonia manicata* Deshayes, 1853. Fig. 23: *Tritonia striata* Haefelfinger, 1963. Fig. 24: *Diaphorodoris papillata* Portmann et Sandmeier, 1960. Fig. 25: *Diaphorodoris luteocincta* var. *alba* (M. Sars, 1870). Fig. 26: *Polycera quadrilineata* (O. F. Müller, 1776). Fig. 27: *Felimare fontandraui* (Pruvot-Fol, 1951).



Figures 28–33. Fig. 28: *Felimare picta* (Schultz in Philippi, 1836). Fig. 29. *Felimare tricolor* (Cantraine, 1835). Fig. 30: *Felimida krohni* (Vérany, 1846). Fig. 31: *Felimida luteorosea* (Rapp, 1827). Fig. 32: *Peltodoris atromaculata* Bergh, 1880. Fig. 33: *Phyllidia flava* Aradas, 1847.

DISTRIBUTION. This is one of the most common species of the Mediterranean Sea. It is also recorded from Western Atlantic Ocean from Portuguese coasts to Canary Islands.

Familia PHYLLIDIIDAE Rafinesque, 1814  
Genus *Phyllidia* Cuvier, 1797

### 23. *Phyllidia flava* Aradas, 1847 (Fig. 33)

ECOLOGY. This interesting sea slug has a characteristic body colour that can camouflage it when it is associated to sponges like *Axinella cannabina* (Esper, 1794), *A. polypoides* Schmidt, 1862 and *Acanthella acuta* Schmidt, 1862. It has been known to feed on the latter sponge.

DISTRIBUTION. This species is rare and distributed throughout the Mediterranean Sea, it has been also recorded from the Canary Islands.

## ACKNOWLEDGEMENT

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## ***Barycypraea teulerei* (Cazenavette, 1845) (Gastropoda Cypraeidae): a successful species or an evolutionary dead-end?**

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### **ABSTRACT**

*Barycypraea teulerei* (Cazenavette, 1845) (Gastropoda Cypraeidae) is an unusual cowrie species, showing remarkable adaptations to an uncommon environment. It lives intertidally on flat sand/mud salt marshes, in a limited range, in Oman. On Masirah Island, humans probably drove it to extinction because of shell collecting. A new population, with a limited range, has recently been discovered, and this article describes observations I made on site in 2014. Evolution shaped this species into a rather specialized and successful life, but has also put it at risk. *Barycypraea teulerei* is well adapted to survive in its habitat, but at the same time is easily visible and accessible to humans, and this puts it at high risk of extinction. Evolution is indeed a blind watchmaker that ‘has no vision, no foresight, no sight at all’. And *B. teulerei* was just plain unlucky to encounter our species on its journey on our planet.

### **KEY WORDS**

Cypraeidae; *Barycypraea teulerei*; Biology; Evolution; Blind Watchmaker.

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### **INTRODUCTION**

“Natural selection, the blind, unconscious, automatic process which Darwin discovered, and which we now know is the explanation for the existence and apparently purposeful form of all life, has no purpose in mind. It has no mind and no mind's eye. It does not plan for the future. It has no vision, no foresight, no sight at all. If it can be said to play the role of watchmaker in nature, it is the blind watchmaker”.

R. Dawkins, The Blind Watchmaker, 1986.

*Barycypraea teulerei* (Cazenavette, 1845) (Gastropoda Cypraeidae) (Fig. 1) is one of only two relic species of the genus *Barycypraea* Schilder, 1927, along with the South African *Barycypraea fultoni*

(Sowerby III, 1899) (Fig. 2). This genus is characterized by squat, heavy shells with a roughly triangular/pyriform shape. The mantle is always thin and almost transparent, whitish or pale brown, with little (*B. fultoni*) or no papillae (*B. teulerei*). Both species appear to be well adapted to sand and/or mud bottoms, although at very different depths. *Barycypraea fultoni* is a deep water species (Bergonzoni, 2012) while, as we will see in detail, *B. teulerei* is an intertidal one.

The genus comprises few fossil species, among them *B. ziestmani* Liltved et Le Roux, 1988 from the Alexandria Formation (Neogene), Port Elizabeth, S. Africa (Liltved, 2000), and the *B. caputvi-perae* species-complex from Indonesia (Miocene). The genus *Barycypraea* is morphologically and genetically linked to the genus *Zoila* Jousseaume,



1884, which is endemic to Western and Southern Australia. In this sense, the entire evolution of this cowrie lineage has always been strictly related to the Indian Ocean basin. The supposed similarity to the Venezuelan/Colombian *Muracypraea mus* (Linnaeus, 1758) and other allied fossil species of the Caribbean genus *Siphocypraea* Heilprin, 1897 [f.i. *S. problematica* (Heilprin, 1887)], seems not fully supported by molecular studies (Meyer, 2004).

### A STORY OF A ONCE RARE SPECIES

*Barycypraea teulerei* was once an extremely rare species. In 1964, only 35 specimens were present in European collections (Schilder, 1964). Since 1969, only guesses were available about its distribution and habitat, since no one had ever reported a precise locality for the species. Specimens were labeled from different localities, including the Persian Gulf, Hormuz Strait, Aden, Arabian Sea, Red Sea, Port Sudan etc. (see Scali, 2013 for a detailed list), but in fact, no one knew where this species came from.

In March 1969, the very first specimens of *B. teulerei* were collected at Masirah Island (wrongly reported as Museera Island; Cross, 1969), a very remote island along the Oman coastline. *Barycypraea teulerei* appeared to live in very shallow water on sand/mud beds, and even outside the water during low tide. Since then, several malacologists made their way to Masirah to obtain specimens (see f.i. Williams, 1969; Luther, 1972; Charter, 1983) which soon became available for study and collection. One of the main sources was actually Dr. Donald 'Don' T. Bosch, who had a long service as a surgeon for the Sultanate of Oman. Dr. Bosch was the only surgeon in the entire country of 1.5 million people, and contributed to the modernization of health care in Oman. In recognition of his achievements, the Sultan of Oman awarded him with the "Order of Oman" in 1972. Don was also an extensive shell collector and a pioneer of Oman malacology. Many Oman species have been named by or after him (e.g. *Conus boschi* Clover, 1972, *Cymatium boschi* Abbott et Lewis, 1970, etc.), and he also dedicated some to his wife Eloise (e.g. *Acteon eloisae* Abbott, 1970). Because of Don Bosch and other shell collectors, thousand of specimens were easily available

for a while, and the species became quite common in collections.

Eventually, in the early 90s, new fresh-collected *B. teulerei* began to disappear. By then, many collectors traveled to Masirah to collect specimens, without success. The species seemed to have simply vanished, probably due to over-collection and the relative ease of finding specimens by simply walking the flat beaches of the Island. Rumors were growing that this species had to be considered extinct.

In December 2012, after some unsuccessful trips to Oman, *B. teulerei* was found again by Massimo Scali and his family along the coastline of Oman (Scali, 2013; 2014), in a locality kept secret since then. The population was very healthy, with several thousand specimens freely grazing on a muddy flat bottom. Again, it was confirmed that this species lives in the intertidal zone. At low tide, *B. teulerei* does not hide itself under stones, as most cowries would do, and it is quite often completely exposed. In figure 3 you can see some in situ specimens during the syzyzian tide of 2014.

In December 2014, I was fortunate enough to join Massimo in his field trip to see this species on site. This article is basically a series of observations I've made that I hope will be of interest to the readers. I will discuss some of the aspects of the biology of this species, and I will express some considerations about its evolution.

### THE HABITAT

Once I arrived at the place during the syzyzian tide of December 2014, I soon realized we were in an unusual habitat for a cowrie species. What I saw was basically a muddy salt marsh, covered with patches of algal mats and a few dark gray and orange sponges (Figs. 4, 5). No rock or evident coral to be found for kilometers. The only available hard substrate was a few *Pinna* sp. standing out of the bottom and a few dead bivalve shells. The mud was very anoxic, dark colored and stinking of sulfur. It was hard to walk on, at every step I remained glued in the mud. Despite this environment seeming quite inhospitable, a few minutes walking from the beach I found the first living *B. teulerei*. This mud flat is a relatively large area and we were walking, on average, 10–15 kilometers per day to observe *B.*



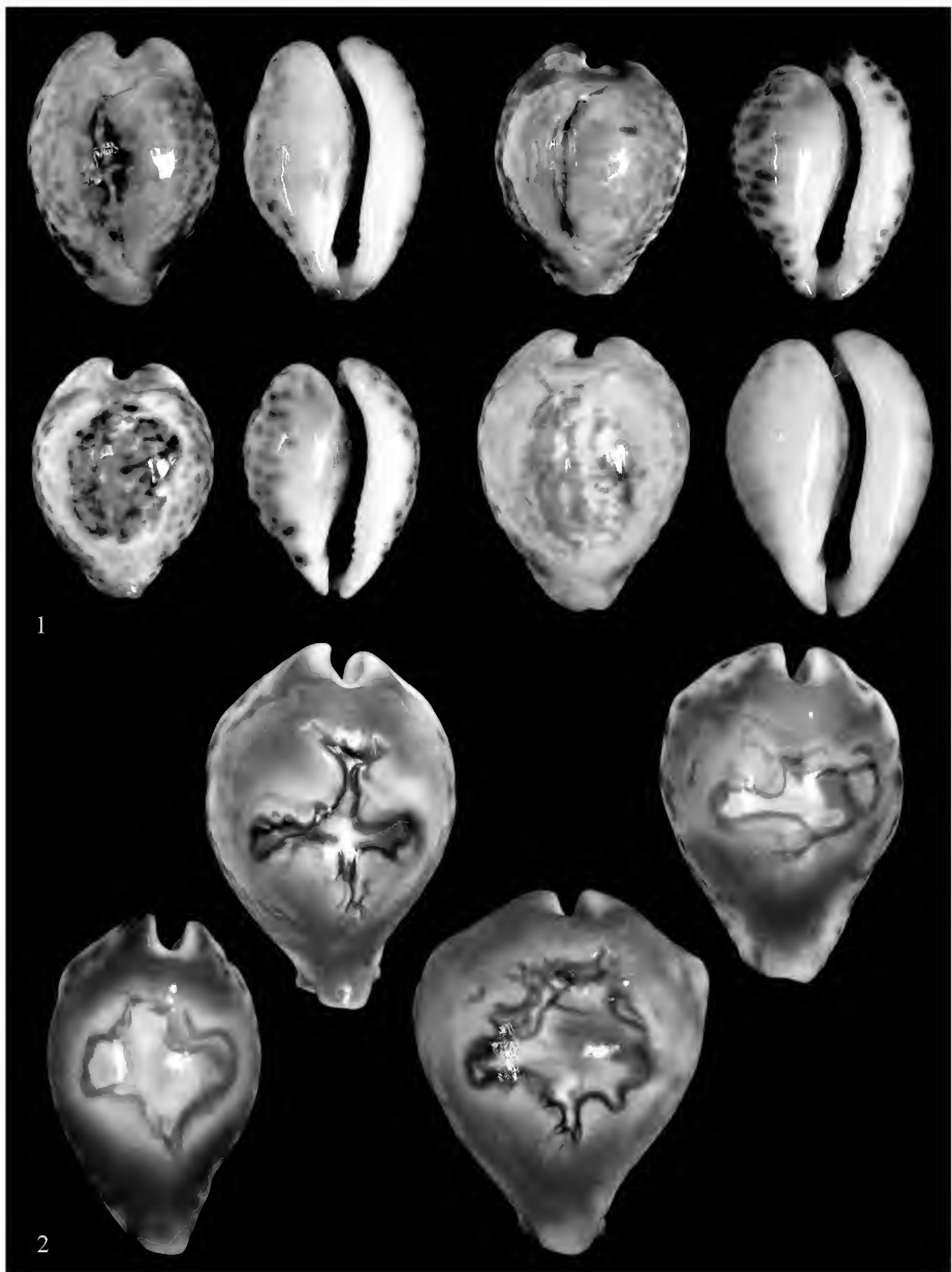


Figure 1. *Barycypraea teulerei*. Examples of variability of pattern of the species. Oman. Photo courtesy Massimo Scali and Beautifulcowries Magazine. Figure 2. *Barycypraea fultoni*. Examples of pattern and variability of the species. Mozambique and South Africa. Photo courtesy Mirco Bergonzoni and Beautifulcowries Magazine.

*teulerei* in situ. The other animals I was able to see were crabs, cuttlefishes, many bivalves, muricids, and some other cowrie species. Nevertheless, *B. teulerei* is by far the most common species in this environment. Its distribution is not even, however. *Barycypraea teulerei* tends to aggregate, and you can find dozens of specimens together in the same patch, then walk for minutes and not find one. What I observed is that the animals are active during the daytime, especially the small ones that I think may be males (see below). In many cases, they are heedless of being completely outside of the water. Walking on the flat for hours, I was also able to ob-

serve a few species of sea birds including small waders, flamingos and seagulls.

In comparing this to the previous known habitat of *B. teulerei* (which I indeed visited), the main difference is that at Masirah Island the sediment is sand, and the bottom is not anoxic. In Masirah, the above-mentioned algal mats and sponges are nowadays very rare, and the area looks more like a big sandy beach with scattered rocky patches. Nevertheless historical records, as well as a few very dead shells, witness that the area once hosted *B. teulerei*. My guess is that, besides collection pressure, there could have been some environmental change.



Figure 3. *Barycypraea teulerei* wandering on a mud flat outside water at syzyzial low tide in December 2014. Oman.



Figure 4. The typical environment, at low tide, where *Barycypraea teulerei* are commonly found. Please note the algal patches. Oman. Figure 5. A close look of the sponge, common in the area, on which *Barycypraea teulerei* was seen eating. Oman.

In my opinion, *B. teulerei* needs the presence of sponges to establish a healthy population. During my observations, I was able to see a *B. teulerei* feeding on a dark gray/black sponge (Fig. 5), so I can confirm this species is spongivorous. However, I cannot exclude it feeding on algae too, but I have not seen any doing so. This is another characteristic that joins *B. teulerei* to the spongivorous *Zoila*.

## REPRODUCTION AND LIFE CYCLE

Two other things are, in my opinion, necessary for *B. teulerei* to establish a healthy population. Firstly, dead bivalve shells. *Barycypraea teulerei* uses these shells to nest its eggs. When a female is brooding eggs (as all cowries do), she hides herself and the eggs on the underside of the valve. Females are hidden by the bivalve shell, but you can spot them because several males are commonly found close to them (Fig. 6). Females, on average, tend to be bigger than males, although this is not always true. Massimo Scali also spotted a male fecundating a female on eggs (Fig. 7). This may be an indication that eggs are fecundated while females lay them, and a reason why males compete for laying females.

Egg clusters are comprised of transparent capsules with brownish eggs inside. Immature capsules contain many eggs, but as development continues, only a few embryos per capsule are found. Embryos are easy to spot because they already have a formed shell (Fig. 8). Likely most of the eggs inside the capsule are only for embryo nutrition (nurse cells or intracapsular cannibalism?). It is therefore evident that this species has direct development and only one (or a few) newborns are hatching from each capsule. Direct development is, in cowries, considered an adaptation when a species depends on a limited food source (in this case sponges), so that newborns hatch close to their food source instead of being spread throughout wide areas as veligers. This direct development is again another similarity to *Zoila*.

When we arrived in December, many specimens were brooding eggs and we seemed to be right in the middle of the reproductive season. Air temperatures in Oman during December are not extremely hot, and during the day can reach 25–30°C. However, at night it can be as cold as 10°C or less.



Figure 6. The typical behavior of a female breeding eggs. Above: the female is hidden under a dead bivalve shells, and two males are trying to fecundate. Below: same animals, after I turned the bivalve to make the female visible. Oman.

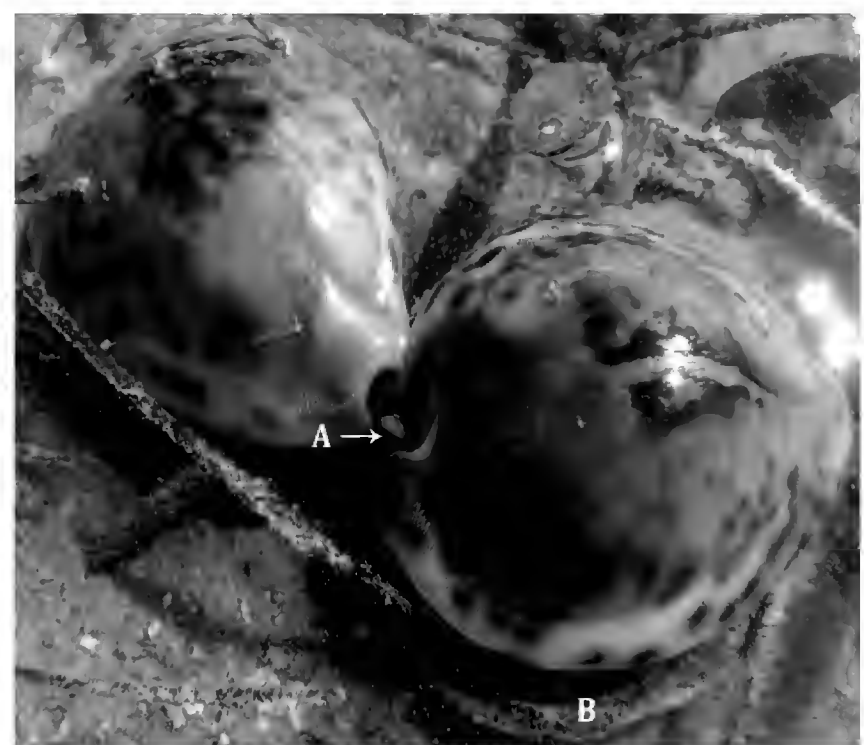


Figure 7. A male *Barycypraea teulerei* fertilizes with his penis (A) a female that sits on a bivalve shell (B). Oman. Photo courtesy Massimo Scali.



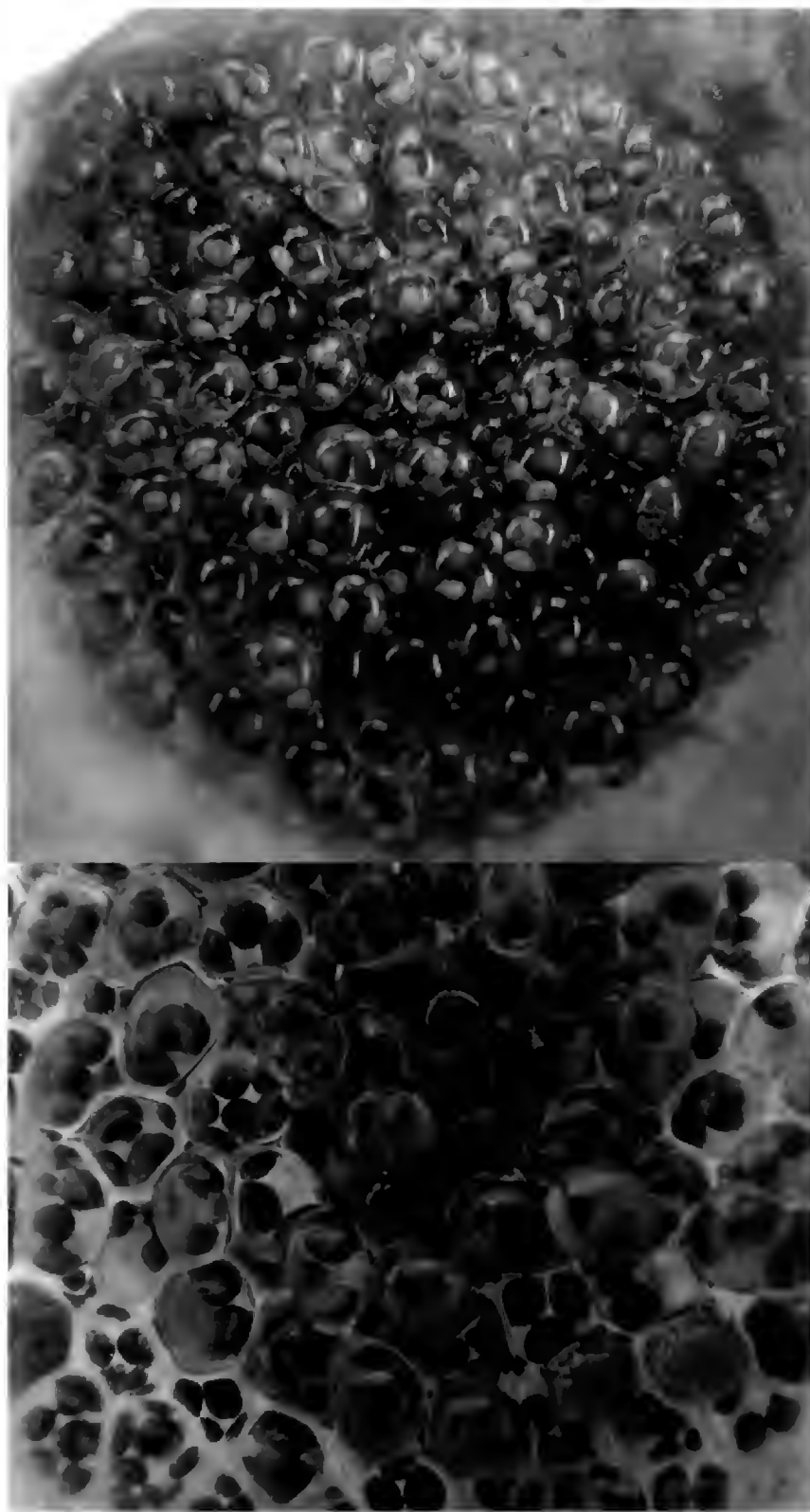


Figure 8. Two views of egg clusters inside bivalve shells. Please note that each capsule may contain different numbers of brownish eggs, and as soon as the embryos get bigger, the number of them decreases. Intracapsular cannibalism? Oman. Photo courtesy Massimo Scali and Beautifulcowries Magazine.

Our time at the site was basically the coldest part of the year, and I guess this is the main reason why *B. teulerei* reproduce during winter. This species is intertidal, so it is strongly influenced by solar heat and desiccation, and winter is the time of the year in which that is least likely to happen. The mud itself may also help in maintaining mollusk wetness and lowering temperature during air exposure. Moreover, water patches and little canals are still present in the mud flat, and some specimens (espe-

cially males) seem to take refuge in these when the tide is very low. Finally, almost no specimen showed an expanded mantle, and this is certainly a behavior for retaining moisture and reducing dehydration.

Another surprising observation, confirmed by previous reports at Masirah, is that we couldn't find any juvenile *B. teulerei*. All specimens were adults or, slightly sub-adult. Another important observation is that while adults are very visible and active, sub-adults are more mimetic and tend to hide below the algal mats. The fact that no young *B. teulerei* were found points sharply to the possibility that this species has a synchronized life cycle, and all reproducing mollusks found are the ones born from eggs of the previous year. Moreover, another observation is important: although *B. teulerei* shells are very heavy, no shell seems gerontic and most of them are undamaged. It seems likely they had no time to be damaged, and maybe this is because all those reproducing shells are just one year old and reached sexual maturity only a few weeks before we arrived.

If my hypothesis is correct, this would mean that *B. teulerei* is a cowrie with a very fast life cycle. Soon after December/January they hatch as small crawling snails. The snails, having thin shells, protect themselves from predators and desiccation by hiding inside the algal mats, which are actually quite intricate, and I guess these may also help in cooling the mollusks during the hot season low tides. Sponges are too small to be a suitable refuge even for the youngest snails. They develop this way until the beginning of the next reproductive season, when they complete development and start wandering for dead bivalve shells (if female) or other females (if males). Again, this peculiar life cycle, if confirmed, coincides quite remarkably with *Zoila*. Actually, *Zoila* newborns are very cryptic, as they hide inside sponges as protection from predation, and they only venture out into the open during reproductive season, when they reach adulthood and shells get thicker. *Zoila friendii*, for instance, broods eggs in the open (personal observation) just as *B. teulerei* does.

The complete development of *B. teulerei* is therefore spanning along the hot season. Oman is very hot during summer, easily reaching 40°C or more. I may imagine that, especially during low tide, the water could reach a very high temperature. Please

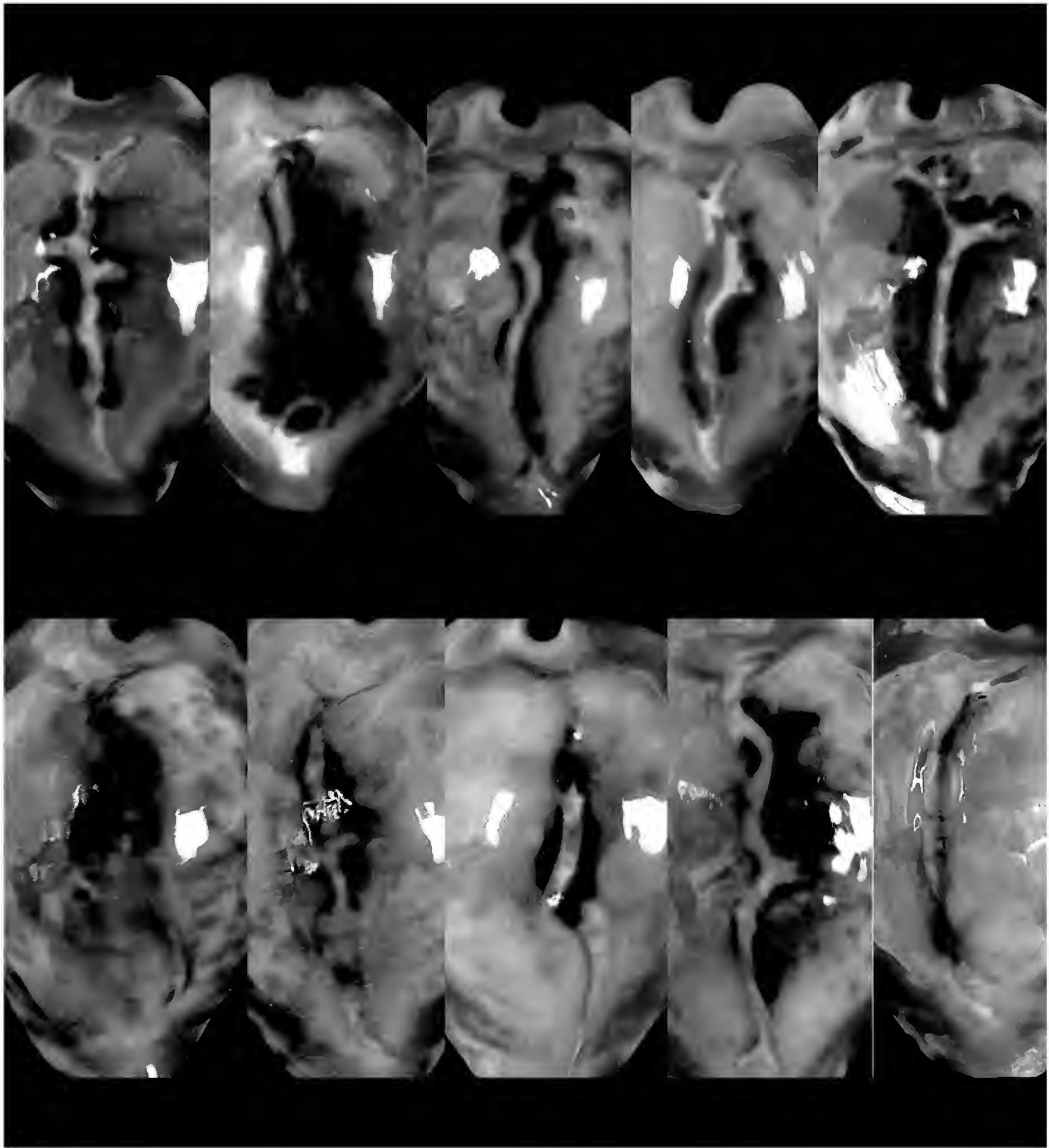


Figure 9. Examples of the variability of the dorsum in *Barycypraea teulerei*, some resembling a false aperture. Oman.

remember that this is a large lagoon flat and that the open ocean, which may be cooler, is quite distant. It is quite unbelievable, but apparently young *B. teulerei* are able to deal with these harsh conditions and reach adulthood with good success. A possibility is that *B. teulerei* migrates into shallow waters only to reproduce, and lives most of the year in deeper waters, where conditions are more stable. I

do not think this is the case, because this species is not capable of fast movement, and the mud flat is several kilometers wide. Plus, I found most individuals very far from the deeper areas (actually the closer we searched to the open ocean, the less specimens were found). Moreover, it is unlikely that young *B. teulerei* are able to migrate back to the deeper water during their development, when they



are most vulnerable due to their thin shells. We also dredged for a few hours along the edge of the flat at a depth of 5–10 meters, and we found no *B. teulerei*, not even dead ones.

Finally, what is the fate of the specimens that reached the first reproductive season? Do they survive to the next year? Is this species annual or not? Hard to say, but the fact that I could see very few damaged and no gerontic shells suggests that this species is rather annual, and after reproduction *B. teulerei* dies. If this is true, the population renews itself every year. It may seem strange that a mollusk forms such a hard, heavy shell in only one year, but there is no biological reason to disregard this hypothesis. On the other hand, it is true that we found very few dead shells, and there should be many more if they all die each year. It is also true that they can be easily burrowed into the soft mud bottom, so they would easily disappear. Nevertheless some dead shells are found beached as well.

## PREDATION

How does *B. teulerei* deal with predators? As we mentioned, this species lives in open sand/mud flats, and they do not hide when adult. Moreover, several hundred specimens are found in relatively small areas. *Barycypraea teulerei* actually seems quite a successful species and, in fact, it is by far the most common cowrie in that particular habitat. Its behavior is quite the opposite of other cowries inhabiting the same area, f.i. *Naria turdus* (Lamarck, 1810) and *Palmadusta lentiginosa* (J.E. Gray, 1825), which are found hiding inside the algal coating of the numerous *Pinna* sp. found on the muddy bottom. And this is not because they are smaller, since some local *N. turdus* may be as big as *B. teulerei*, and with a similarly thick shell.

Among candidate predators, I may mention seagulls and crabs, which are common in the area, as well as other mollusks. However, very few shells (almost none) show signs of predation, and I have not seen any cracked shells on site or beached. Dead shells are also very rare, and when found, they do not show any sign of attack. It seems that predators are completely ignoring *B. teulerei*, an observation that was quite puzzling. Why should this species not

be predated, and why does it actually seem to ignore predators? Is *B. teulerei* toxic, poisonous, or have a disgusting taste? Hard to say, but as far as I know, no toxic cowrie has ever been reported in literature. It is not unconceivable that perhaps they become toxic, repellent or disgusting by absorbing substances from their food sponges. Only targeted chemical analyses would possibly solve this issue.

Some clues may also come from the shell. As mentioned, *B. teulerei* has a very heavy shell. Its thickness is certainly an adaptation to prevent cracking by fishes, crabs or sea birds, as well as drilling by muricids or naticids. Moreover, its squat shape might also be an adaptation to perfectly adhere it to the bottom (as in many other cowries). However, I may also argue that the peculiar pattern of the dorsum could have an adaptive function, although this is just a guess. In fact, even if the dorsum is characterized by a variable pattern (basically no two specimens are alike), most shells show a neat double dorsal line, framing a central groove, especially when the shell is thicker. More uncommonly, they show a dark blotch in the middle of the dorsum. Other kinds of patterns are rarer. In figure 9 you can see an overview of the variability of the dorsal patterns. Contrarily to the dorsum, the mouth is quite wide and uncolored. Considering all this, my guess is that the flashy dorsal color in this species might be either an aposematic coloration (in case the mollusk is toxic or has a bad taste), or, maybe, could represent a sort of ‘false aperture’ that may distract sea birds from the vulnerable parts of the animal. I may imagine seabirds being fooled and peck at the dorsum of the cowrie, which is actually a very hard part of the shell, completely disregarding the real aperture, where the mollusk would be more vulnerable. Of course this is just a guess, but it is of course not the first such case known in nature: for instance, you may find something similar in false eyes of fishes, which are adaptations to drive predators’ attacks to parts of the body that are less sensitive or critical for survival.

Finally, please also note that this species has no teeth along its aperture, a characteristic that is very rare in cowries, even if some specimens may have some little denticles. Teeth in cowries have a particular function, i.e. to narrow the aperture to prevent attacks from predators, since cowries have no operculum. Evidently this species has no need

for teeth, and teeth, which are found in all other *Barycypraea*, are on their way to being lost. This is a very well known evolutionary process: no selective constraints (i.e. no need for teeth) allow accumulation of mutations, which result in the gene products having less or no function (i.e., the genes or the proteins involved in teeth production being partially or wholly inactivated).

### AN EVOLUTIONARY DEAD END?

All this considered, *B. teulerei* shows a plethora of remarkable adaptations to a very specific environment, which makes this species an outlier among cowries: i) it lives in the intertidal zone on sand/mud flats, where other cowries are rarer; ii) it is active during the day, at variance to other cowries; and iii) it is strictly dependent on a specific habitat and food source. Nevertheless it performs quite well when all these conditions are present, so we can say that this species appears very well adapted to its environment. Evolution has done “a good job” with this species. And, in fact, *B. teulerei* has no significant predators, at least when they are adult and freely grazing and mating in the open.

On the other hand, its distribution range seems quite limited, maybe because of its specialist way of life. The absence of free-swimming larvae is certainly another concurring factor. We tried to find *B. teulerei* elsewhere along the Oman coast, with no success, although more research needs to be done. Unfortunately, the very limited distribution makes this species a highly vulnerable one.

Actually the main concern for the survival of *B. teulerei* does not come from predators, but from humans. It was quite bad luck for *B. teulerei* to find a species collecting it in large numbers for its beauty, rather than for its taste. And it was bad luck indeed that this species is commercially valuable to collectors. The limited range does the rest. The story of the Masirah population teaches us that *B. teulerei* is indeed in high danger of extinction. That is why the new locality should absolutely remain secret, and I am not giving any precise indication as to where it is. It is also my opinion that this species should be protected by law.

The life history of *B. teulerei* is, no doubt, a remarkable one. Evolution shaped this species to a

rather specialized and successful life. At the same time, it has put *B. teulerei* at risk. Evolution is a blind process and of course it could not foresee that, at a certain point, this species would have encountered another one: humans, predating it for its shine, beauty and striking colors. Evolution shaped *B. teulerei* to survive in its habitat, but at the same time made it so easily accessible to humans, and its highly specialized life puts it at risk of extinction. Evolution is indeed a blind watchmaker that ‘has no vision, no foresight, no sight at all’ (Dawkins, 1986). And *B. teulerei* was just plain unlucky to encounter our species during its journey on our planet.

### ACKNOWLEDGMENTS

I wish to thank you very much Massimo Scali (Imola, Italy) for giving me the opportunity to visit and observe on site the new population of *B. teulerei* in Oman, and for providing some of the pictures. I also wish to thank very much the organizers of the VIII Pontine Malacological Congress, Silvia Alfinito and Bruno Fumanti (Sabadia, Italy), as well as the Malakos 2002 association and members, for inviting me to talk about *B. teulerei*. Finally, my acknowledgement goes to Federico Plazzi (Bologna, Italy) and Rex Stilwill (Grand Rapids, MI, USA), for their review of the manuscript.

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# Contribution to the knowledge of the molluscan thanatocoenosis of Zannone Island (Pontine Archipelago, Latium, Italy). Additional reports

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## ABSTRACT

In this second paper concerning the molluscan fauna of Zannone Island (Pontine Archipelago, Italy) one sediment sample collected by scuba diving at a depth of 36.5 meters at SW of the isle was investigated. Altogether, 47 taxa, not yet reported for Zannone, were identified, bringing the total number of the molluscan thanatocoenosis of the island at 327 taxa.

## KEY WORDS

Mollusca; thanatocoenosis; Zannone Island; Italy.

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## INTRODUCTION

In a previous paper on the Mollusca of Zannone Island, Fumanti (2014) reported 280 malacological taxa. Recently prof. Riccardo Lubrano has provided one of us (I. N.) with a sediment sample collected on August 11th 2013 by means of scuba diving by Mr. Nino Baglio at 36.5 m depth SW of Zannone Island. The study of the sample has led to the identification of several taxa, 47 of these, representing an increase of 14.4 % of the total, were not previously reported.

Finally, thanks to the finding of *Spinoaglaja wilpretii* (Ortea, Bacallado et Noro, 2003) by Romani & Pagli (2014), the molluscan thanatocoenosis of the Isle of Zannone consists now of 327 taxa. Furthermore, in this paper, other species, indicated with an asterisk, already reported in Fumanti (2014) have been added with revised and updated nomenclature recording the latest publication.

## RESULTS

### *Taxonomic list*

Classis GASTROPODA Cuvier, 1797  
Ordo PATELLOGASTROPODA Lindenberg, 1986  
Familia LOTTIIDAE Gray, 1840  
Genus *Tectura* Gray, 1847

### *Tectura virginea* (O.F. Müller, 1776)

Ordo VETIGASTROPODA Salvini-Plawen, 1980  
Familia SCISSURELLIDAE Gray, 1847  
Genus *Sinezona* Finlay, 1926

### *Sinezona cingulata* (O.G.Costa, 1861)

Familia SKENEIDAE Clark, 1851  
Genus *Skenea* Fleming, 1825

### *Skenea serpuloides* (Montagu, 1808)

Ordo CAENOGASTROPODA Cox, 1960  
 Familia SILIQUARIIDAE Anton, 1838  
 Genus *Petalopoma* Schiapparelli, 2002

***Petalopoma elisabettae*** Schiapparelli, 2002

Familia SKENEOPSIDAE Iridale, 1815  
 Genus *Skeneopsis* Iridale, 1915

***Skeneopsis planorbis*** (O. Fabricius, 1780)

Familia JANTHINIDAE Lamarck, 1822  
 Genus *Janthina* Röding, 1798

***Janthina pallida*** W. Thompson, 1840

Familia RISSOIDAE J.E. Gray, 1847  
 Genus *Alvania* Leach in Risso, 1826

***Alvania dictyophora*** (Philippi, 1844) group

NOTES. Actually this species is under investigation by Bruno Amati (Rome).

Genus *Setia* H. Adams et A. Adams, 1852

***Setia turriculata*** Monterosato, 1884

Familia CYPRAEIDAE Rafinesque, 1815  
 Genus *Naria* Broderip, 1837

***Naria spurca*** (Linnaeus, 1758)

Familia LIMACINIDAE Gray, 1840  
 Genus *Thielea* Strebel, 1908

***Thielea inflata*** (d'Orbigny, 1836)

Genus *Limacina* Bosc, 1817

***Limacina trochiformis*** (d'Orbigny, 1836)

Familia PERACLIDAE Tesch, 1913  
 Genus *Peracle* Forbes, 1844

***Peracle reticulata*** (d'Orbigny, 1836)

Familia MURICIDAE Rafinesque, 1815  
 Genus *Dermomurex* Monterosato, 1890

***Dermomurex scalaroides*** (Blainville, 1826)

Genus *Murexsul* Iridale, 1915

***Murexsul aradasii*** (Monterosato in Poirer, 1883)

Familia MITROMORPHIDAE Casey, 1904  
 Genus *Mitromorpha* Carpenter, 1865

\****Mitromorpha columbellaris*** (Scacchi, 1836)

\****Mitromorpha olivoidea*** (Cantraine, 1835)

NOTES. The nomenclature of the two species belonging to the genus *Mitromorpha*, previously reported in Fumanti (2014) are here updated according to Amati et al. (2015).

Ordo HETEROSTROPHA P. Fischer, 1885  
 Familia OMALOGYRIDAE G.O. Sars, 1878  
 Genus *Omalogyra* Jeffreys, 1859

***Omalogyra atomus*** (Philippi, 1841)

Genus *Ammonicera* Vayssière, 1893

***Ammonicera*** cfr. ***andresi*** Oliver et Rolán, 2015

\****Ammonicera*** cfr. ***fischeriana*** (Monterosato, 1869)

***Ammonicera*** cfr. ***superstriata*** Oliver et Rolán, 2015

NOTES. The determination of the species belonging to the genus *Ammonicera*, according to the recent review of this genus (Oliver & Rolán, 2015) and without SEM observations, has led to considerable difficulties and is proposed here with a wide margin of uncertainty.

Familia PYRAMIDELLIDAE Gray, 1840  
 Genus *Parthenina* Bucquoy, Dautzenberg et Dollfus, 1883

***Parthenina clathrata*** (Jeffreys, 1848)

\****Parthenina dollfusi*** (Kobelt, 1903)

\****Parthenina emaciata*** (Brusina, 1866)

\****Parthenina interstincta*** (J. Adams, 1797)

\****Parthenina monozona*** (Brusina, 1869)

\****Parthenina moolenbeecki*** (Amati, 1987)

\****Parthenina penchynati*** (Bucquoy, Dautzenberg et Dollfus, 1883)

***Parthenina suturalis*** (Philippi, 1844)

NOTES. As regards to Pyramidellidae we decided to include the full list of the genera and species



reported for Zannone (both in this paper and in Fumanti, 2014) with the nomenclature updated according to Giannuzzi-Savelli et al. (2014).

Genus *Folinella* Dall et Bartsch, 1904

\**Folinella excavata* (Philippi, 1844)

Genus *Odostomella* Bucquoy, Dautzenberg et Dollfus, 1883

\**Odostomella doliolum* (Philippi, 1844)  
*Odostomella bicincta* (Tiberi, 1868)

Genus *Euparthenia* Thiele, 1931

\**Euparthenia humboldti* (Risso, 1826)

Genus *Eulimella* Forbes et Mac Andrew, 1846

*Eulimella acicula* (Philippi, 1836)  
\**Eulimella ventricosa* (Forbes, 1844)

Genus *Odostomia* Fleming, 1813

\**Odostomia carrozzai* Van Aartsen, 1987  
\**Odostomia eulimoides* Hanley, 1844  
\**Odostomia lukisii* Jeffreys, 1859  
\**Odostomia scalaris* Mac Gillivray, 1843  
*Odostomia striolata* (Forbes et Hanley, 1850)  
\**Odostomia turrita* Hanley, 1844  
\**Odostomia unidentata* (Montagu, 1803)

Genus *Megastomia* Monterosato, 1884

*Megastomia alungata* (Nordsieck, 1972)  
\**Megastomia conoidea* (Brocchi, 1814)

Genus *Ondina* De Folin, 1870

\**Ondina vitrea* (Brusina, 1866)  
*Ondina scadens* (Monterosato, 1844)

Genus *Pyrgostylus* Monterosato, 1884

\**Pyrgostylus striatulus* (Linnaeus, 1758)

Genus *Turbonilla* Risso, 1826

\**Turbonilla pumila* G. Seguenza, 1876

Genus *Careliopsis* Morch, 1875

*Careliopsis modesta* (De Folin, 1870)

Familia MURCHISONELLIDAE Casey, 1904

Genus *Ebala* Gray, 1847

*Ebala pointeli* (De Folin, 1867)

Familia CIMIDAE Warén, 1993

Genus *Cima* Chaster, 1896

*Cima cylindrica* (Jeffreys, 1856)  
*Cima minima* (Jeffreys, 1858)

Familia TOFANELLIDAE Bandel, 1995

Genus *Graphis* Jeffreys, 1867

*Graphys albida* (Kanmacher, 1798)

Ordo CEPHALAPSIDEA Fischer, 1883

Familia PLEUROBRANCHIDAE Gray, 1827

Genus *Berthella* Blainville, 1824

*Berthella* sp.

Familia RETUSIDAE Thiele, 1925

Genus *Volvulella* Newton, 1891

*Volvulella acuminata* (Broguière, 1792)

Familia PHILINIDAE Gray, 1850

Genus *Philine* Ascanius, 1772

*Philine catena* (Montagu, 1803)

*Philine angulata* Jeffreys, 1867

Genus *Petalifera* Gray, 1847

*Petalifera* cf. *gravieri* (Vayssiere, 1906)

Familia AGLAJIDAE Pilsbry, 1895

Genus *Spinoaglaja* Ortea, Moro et Espinosa, 2007

*Spinoaglaja wilpretii* (Ortea, Bacallado et Noro, 2003)

NOTES. Species reported on the basis of one specimen (3.3 mm) devoid of soft part at 36 m of depth.

Classis BIVALVIA Linnaeus, 1758  
 Ordo SOLEMYOIDA Dall, 1889  
 Familia NUCULIDAE Gray, 1824  
 Genus *Nucula* Lamarck, 1799

*Nucula* sp. (juv.)

Ordo MYTILOIDA Férussac, 1822  
 Familia MYTILIDAE Rafinesque, 1815  
 Genus *Crenella* T. Brown, 1827

*Crenella pellucida* (Jeffreys, 1850)

Genus *Dacrydium* Torell, 1859

*Dacrydium hyalinum* Monterosato, 1875

Familia ANOMIIDAE Rafinesque, 1815  
 Genus *Pododesmus* Philippi, 1837

*Pododesmus* sp.

Ordo LUCINIDAE Gray, 1854  
 Familia LUCINIDAE Fleming, 1828  
 Genus *Anodontia* Link, 1807

*Anodontia fragilis* Philippi, 1836

Genus *Loripes* Poli, 1791

*Loripes lucinalis* (Lamarck, 1818)

Familia MONTACUTIDAE W. Clark, 1855  
 Genus *Montacuta* Turton, 1822

*Montacuta substriata* (Montagu, 1808)

Ordo VENEROIDA Gray, 1854  
 Familia CARDIIDAE Lamarck, 1809  
 Genus *Laevicardium* Swainson, 1846

*Laevicardium crassum* (Gmelin, 1791)

Familia TELLINIDAE Blainville, 1814  
 Genus *Arcopagia* Brown, 1877

*Arcopagia balaustina* (Linnaeus, 1758)

Familia PSAMMOBIIDAE Fleming, 1828  
 Genus *Gari* Schumacher, 1817

*Gari costulata* Turton, 1822  
*Gari depressa* (Pennant, 1777)

Classis SCAPHOPODA Bronn, 1862  
 Ordo DENTALIIDAE da Costa, 1776  
 Familia DENTALIDAE J.E. Gray, 1834  
 Genus *Antalis* H. Adams et A. Adams, 1854

*Antalis vulgaris* da Costa, 1778

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# Terrestrial gastropods (Mollusca Gastropoda) from Lepini Mountains (Latium, Italy): a first contribution

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## ABSTRACT

Lepini Mountains are a calcareous massif that forms the southern pre-Apennines of Latium (Italy), reaching a maximum altitude of 1536 m. Notwithstanding their central position and the low height reached, the malacofauna of Lepini Mountains has been long neglected and species composition was never reported so far. In this contribution, a preliminary investigation of the terrestrial gastropods (Mollusca Gastropoda) occurring in the Lepini Mountains is reported. At least 43 species are recorded. Several species already reported from Central Apennines occur. The most remarkable findings include a hitherto unrecorded population of *Medora* sp. (Clausiliidae) and the occurrence of two distinct forms ascribable to *Jaminia quadridens* s.l.

## KEY WORDS

Terrestrial gastropods; biodiversity; Lepini Mountains; Italy.

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## INTRODUCTION

Lepini Mountains, together with Aurunci and Ausoni Mountains, form the southern pre-Apennines of Latium (Italy). They are positioned about 50 km SE of Rome and extend in NE-SW direction (Fig. 1). They are separated from Central Apennines by the Sacco Valley and face the Pontine alluvial plain in the south. Lepini Mountains are comprised of two parallel chains directed in NE-SW direction, separated by the deep Montelanico-Carpineto-Maenza tectonic line. The western chain is comprised by Mount Lupone (1378 m) and Mount Semprevisa group (1536 m, the highest peak), whereas the eastern chain quickly slopes down to the Sacco Valley and is comprised of Mount Gemma, Mount Malaina, Mount S. Marino and Mount Alto, all of which reach heights around 1400 m.

Lepini Mountains are mainly comprised of limestone of Cretaceous age (Sani et al., 2004). The whole massif shows to intense karst phenomena. As a consequence, in the Lepini Mountains no permanent water body occurs, whereas several springs appear at the base of the massif, the best known of which gives rise to the Oasis of Ninfa (Amori et al., 2002).

The vegetation is mainly comprised of holm oak, chestnut and mixed woods at medium-low altitudes and beech forests at medium-high altitudes. Large portions of territory are occupied by grassland mainly used as pasture.

The invertebrate fauna of Lepini Mountains have been studied in some detail with regard to arthropods (Corsetti et al., 2015). Several studies focused on hypogean fauna (Sbordoni, 1971; Latella, 1995; Nardi et al., 2002). Moreover, some endemisms have been reported (Sbordoni, 1971;

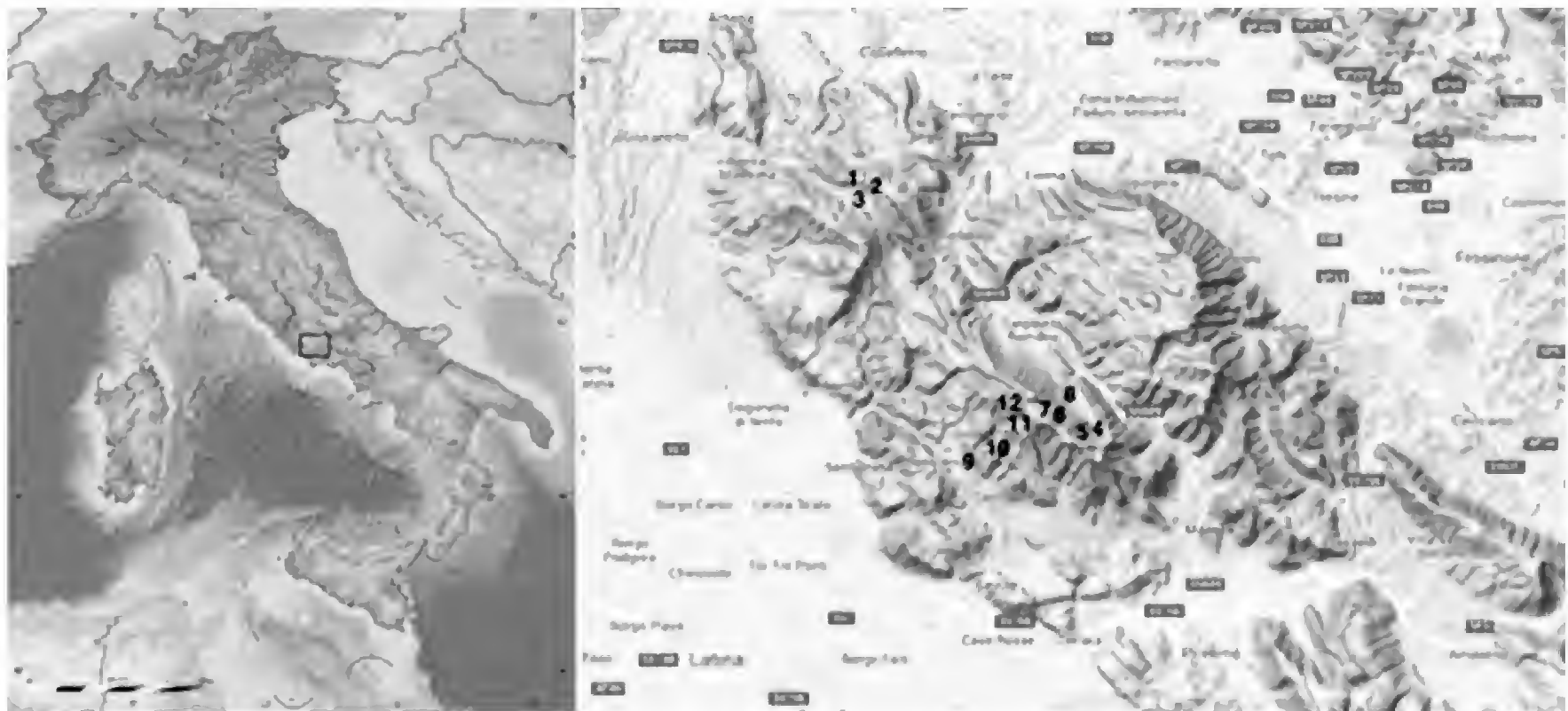


Figure 1. Studied area: Lepini Mountains (southern Latium, Italy).  
Numbers indicate the sampled stations listed in Table 1.

Stn.	Locality	Coordinates	Alt. (m)	Environment
1	Pass to Campo di Segni	41.672649° N, 12.987930° E	1015	Pasture with stones
2	After pass to Campo di Segni	41.670720° N, 12.993717° E	960	Rocks with low vegetation
3	Close to Campo di Segni	41.667926° N, 12.990029° E	880	Pasture and bushes with stones
4	Mount Erdigheta	41.56410° N, 13.119629° E	1046	Beech forest with rocks
5	Mount Erdigheta	41.562092° N, 13.120613° E	1115	Pasture with stones
6	Mount Semprevisa	41.572228° N, 13.092678° E	1250–1400	Beech forest with rocks
7	Mount Semprevisa, top	41.571147° N, 13.091063° E	1490	Stones on the top
8	Carpineto, Pian della Faggeta	41.575702° N, 13.103665° E	930	Rocks with low vegetation and residuary beeches
9	Bassiano, road to Semprevisa, near the spring	41.552975° N, 13.047529° E	590	Holm oak wood with rocks
10	Bassiano, road to Semprevisa	41.558473° N, 13.059121° E	864	Clearing in holm oak wood
11	Campo Rosello	41.563711° N, 13.077542° E	1174	Pasture with stones
12	Campo Rosello	41.571987° N, 13.072649° E – 41.574551° N, 13.074571° E	1250–1410	Pasture with stones

Table 1. List of the stations: Lepini Mountains (southern Latium, Italy).

Pace, 1975; Magrini, 2005). However, the molluscan fauna of Lepini Mountains was never studied so far. Only four species occurring in hypogean environments were reported (*Discus rotundatus*, *Campylaea planospira*, *Daudebardia brevipes* and *Oxychilus draparnaudi*), none of which strictly hypogean (Latella, 1995).

In this contribution, we report the results of a first survey aimed at assessing the biodiversity of terrestrial gastropods of Lepini Mountains.

## MATERIAL AND METHODS

A total of 12 stations along the western chain have been sampled between April and June 2015 (see Table 1). Sampling was carried out only in natural environments. As a consequence, species recorded only from urban areas, such as *Cornu aspersum* (O.F. Müller, 1774) found in the town of Bassiano, were ruled out. Additionally, freshwater or hypogean environments were not considered. For the nomenclature, we mainly referred to the checklist of the species of the Italian fauna (Bodon et al., 1995; Manganelli et al., 1995, 1998, 2000). For the suprageneric nomenclature, we referred to Bouchet & Rocroi (2005). All specimens here illustrated were collected from the Lepini Mountains. Shell length and width were measured parallel and perpendicular to the axis of the shell, respectively, with calipers to the nearest 0.1 mm.

## RESULTS AND DISCUSSION

At least 44 species of terrestrial gastropods occur in the Lepini Mountains (see Table 2). The most speciose family is the Clausiliidae, with 7 recorded species. The clausiliid *Leucostigma candidescens* is by far the commonest and widespread species, occurring in almost all calcareous outcrops, either exposed or shaded, often associated with other calciophilous species such as *Cochlostoma* cf. *adamii*, *Marmorana signata*, *Granaria apennina* and *Medora* sp. We agree with Fehér et al. (2010) who indicate the species of the genus *Granaria* Held, 1838 occurring in the Italian peninsula as *G. apennina*. *Medora* sp. was found only in a single station inside the beech forest of Mount Semprevisa. The unexpected finding of this population confirms that

the current knowledge of the genus *Medora* H. et A. Adams, 1855 in Italy is far from being exhaustive (Giusti et al., 1986; Nordsieck, 2012; Colomba et al., 2012). *Cochlodina laminata* and *C. bidens* occur in sympatry in the beech forest. According to Opinion 2355, the Apennine species so far known as *Cochlodina incisa* (Küster, 1876) should be indicated as *C. bidens* (Linnaeus, 1758) (Kadolsky, 2009; ICZN, 2015). They are readily distinguished by the development of palatal plicae. In fact, while in the former palatal plicae are truncated at the level of the clausilium, in the latter both the principal and the lower palatal plicae prolong internally. Moreover, an additional intermediate palatal plica often occurs in the latter. *Cochlodina bidens* in Lepini Mountains shows a stout shell also found in specimens from other localities of Latium, such as the holm oak woods of Mount Circeo and Macchia Grande (Fiomicino) (Hallgass & Vannozzi, 2014).

The populations of *Cochlostoma* cf. *adamii* have been studied by Zallot et al. (2015) in the generic revision of the family Cochlostomatidae and assigned to the subgenus *Turritus* Westerlund, 1883. *Cochlostoma adamii* group is comprised of several forms reported with different nominal taxa occurring from Central Apennines to Sicily, whose taxonomy needs to be clarified. The marquis Paulucci (1881) noted the occurrence of forms close to *Pomatias adamii* in the Central Apennines and described “*Pomatias adamii* Var. *Carseolanus*” from Carsoli (Abruzzi). *Cochlostoma* cf. *adamii* from Lepini Mountains is different from *C. cassiniacum* (Saint Simon in Paulucci, 1878) from Cassino and Sterrone (both Latium), though belonging to the same subgenus *Turritus* (Zallot, comm. pers.).

On the whole, the beech forest shows the greatest biodiversity, with 28 recorded species. Among them, there are several species commonly found in beech forests of Central Apennines (Giusti et al., 1985). However, a few of them deserve some comments. *Acicula* sp. was recorded from a worn fragment. The closest finding of this genus is *A. szigethyannae* Subai, 1977 from Val d’Arano (Ovindoli, Abruzzi). Conversely, *Platyla similis* is recorded from several localities of the Italian peninsula. In particular, it has been reported from the neighbouring Aurunci Mountains (Bodon & Cianfanelli, 2008). *Limax* cf. *maximus* appears with different patterns (Figs. 8 and 9). A completely

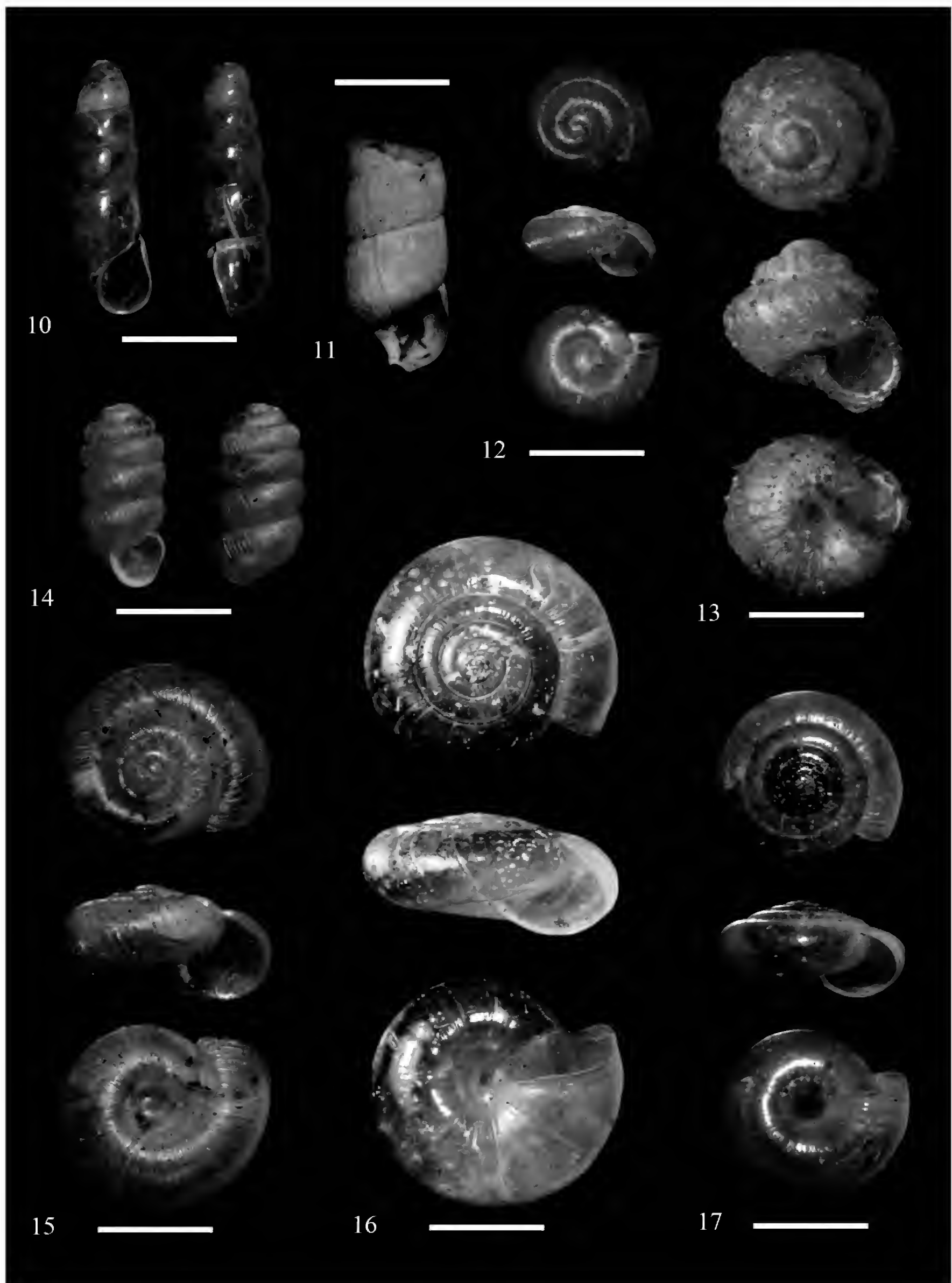


Family	Species	Stn.	Fig.
COCHLOSTOMATIDAE	<i>Cochlostoma</i> cf. <i>adamii</i> (Paulucci, 1879)	4–9, 11, 12	2
ACICULIDAE	<i>Acicula</i> sp.	6	11
	<i>Platyla similis</i> (Reinhardt, 1880)	6	10
POMATIIDAE	<i>Pomatias elegans</i> (O.F. Müller, 1774)	2, 3, 9	
ORCULIDAE	<i>Sphyradium doliolum</i> (Bruguière, 1792)	6, 8	
VALLONIIDAE	<i>Acanthinula aculeata</i> (O.F. Müller, 1774)	8, 9	13
	<i>Gittenbergia sororcula</i> (Benoît, 1857)	6	15
CHONDRINIDAE	<i>Granaria apennina</i> (Küster, 1850)	4, 8	
	<i>Chondrina avenacea</i> (Bruguière, 1792)	6, 9	
VERTIGINIDAE	<i>Truncatellina callicratis</i> (Scacchi, 1833)	9	14
ENIDAE	<i>Jaminia quadridens</i> (O.F. Müller, 1774) (small morphotype)	7, 8	5, 18
	<i>Jaminia quadridens</i> (O.F. Müller, 1774) (large morphotype)	4, 5, 7, 8, 12	4, 19
	<i>Merdigera obscura</i> (O.F. Müller, 1774)	6, 8	
FERUSSACIIDAE	<i>Cecilioides acicula</i> (O.F. Müller, 1774)	9	
SUBULINIDAE	<i>Rumina decollata</i> (Linnaeus, 1758)	1, 3, 9	
CLAUSILIIDAE	<i>Medora</i> sp.	6	20
	<i>Leucostigma candidescens</i> (Rossmässler, 1835)	1–6, 8, 9, 11, 12	3, 21
	<i>Cochlodina laminata</i> (Montagu, 1803)	6	23
	<i>Cochlodina bidens</i> (Linnaeus, 1758)	6	22
	<i>Siciliaria paestana</i> (Philippi, 1836)	3, 5, 6, 9	
	<i>Macrogastra plicatula</i> (Draparnaud, 1801)	6	
	<i>Clausilia cruciata</i> Studer, 1820	6	
PUNCTIDAE	<i>Punctum pygmaeum</i> (Draparnaud, 1801)	6	12
DISCIDAE	<i>Discus rotundatus</i> (O.F. Müller, 1774)	6, 9	
PRISTILOMATIDAE	<i>Vitrea botterii</i> (Pfeiffer, 1853)	4, 6, 8	17
	<i>Vitrea subrimata</i> (Reinhardt, 1871)	6, 8	16
OXYCHILIDAE	<i>Daudebardia rufa</i> (Draparnaud, 1805)	6	6
	<i>Daudebardia brevipes</i> (Draparnaud, 1805)	6	
	<i>Oxychilus</i> cf. <i>draparnaudi</i> (Beck, 1837)	2, 6, 8, 10	
MILACIDAE	<i>Tandonia sowerbyi</i> (Férussac, 1823)	6, 10	7
VITRINIDAE	<i>Semilimacella bonellii</i> (Targioni Tozzetti, 1873)	6	
LIMACIDAE	<i>Limax</i> cf. <i>maximus</i> Linnaeus, 1758	3, 6, 10	8, 9
	<i>Limax</i> sp. A (black)	3, 6, 8	9
	<i>Limax</i> sp. B (brown)	6	
AGRIOLIMACIDAE	<i>Deroceras</i> cf. <i>lothari</i> Giusti, 1973	8	
HYGROMIIDAE	<i>Monacha</i> cf. <i>cantiana</i> (Montagu, 1803)	9	
	<i>Monacha</i> cf. <i>campanica</i> (Paulucci, 1881)	1, 3, 5, 8, 11, 12	
	<i>Cernuellopsis ghisottii</i> Manganelli et Giusti, 1988	1, 4, 5, 7, 8, 11, 12	
	<i>Cernuella cisalpina</i> (Rossmässler, 1837)	10	
	<i>Hygromia cinctella</i> (Draparnaud, 1801)	1	
HELICIDAE	<i>Campylaea planospira</i> Lamarck, 1822	6	
	<i>Marmorana signata</i> (Férussac, 1821)	6, 9, 11	
	<i>Cantareus apertus</i> (Born, 1778)	9	
	<i>Helix ligata</i> O.F. Müller, 1774	1, 3, 12	24

Table 2. List of the species recorded in the sampled stations, Lepini Mountains (southern Latium, Italy).

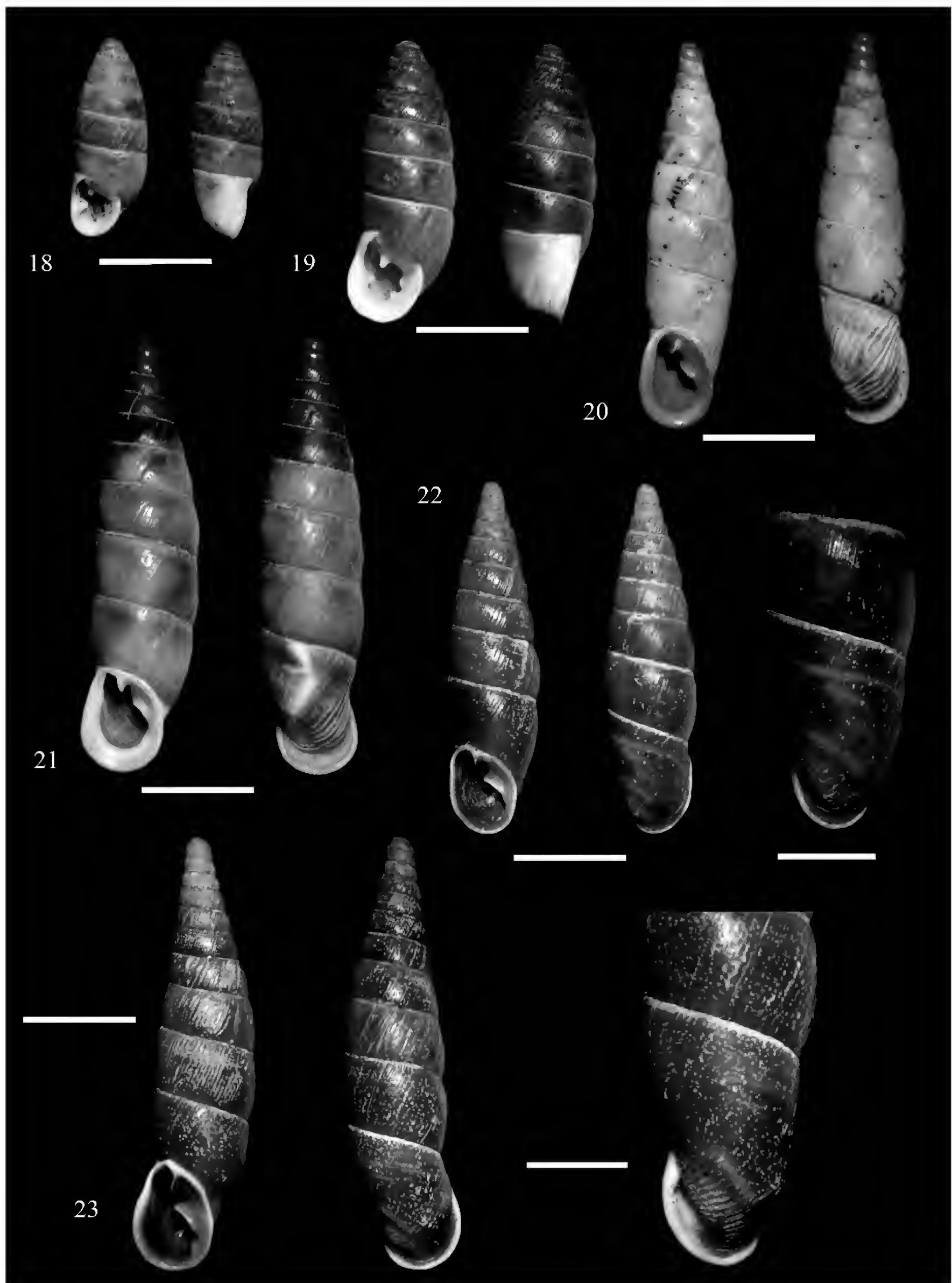


Figures 2–9. Terrestrial gastropods from Lepini Mountains. Fig. 2: *Cochlostoma* cf. *adamii*. Fig. 3: *Leucostigma candidescens*. Fig. 4: *Jaminia quadridens* (large morphotype). Fig. 5: *Jaminia quadridens* (small morphotype). Fig. 6: *Daudebardia rufa*. Fig. 7: *Tandonia sowerbyi*. Fig. 8: *Limax* cf. *maximus*. Fig. 9: *Limax* sp. A (black) and *L.* cf. *maximus*.



Figures 10–17. Terrestrial gastropods from Lepini Mountains. Fig. 10: *Platyla similis*. Fig. 11: *Acicula* sp. Fig. 12: *Punctum pygmaeum*. Fig. 13: *Acanthinula aculeata*. Fig. 14: *Truncatellina callicratis*. Fig. 15: *Gittenbergia sororcula*. Fig. 16: *Vitrea subrimata*. Fig. 17: *Vitrea botterii*. Scale bar: 1 mm.





Figures 18–23. Terrestrial gastropods from Lepini Mountains. Fig. 18: *Jaminia quadridens* (small morphotype). Fig. 19: *Jaminia quadridens* (large morphotype). Fig. 20: *Medora* sp. Fig. 21: *Leucostigma candidescens*. Fig. 22: *Cochlodina bidens*. Fig. 23: *Cochlodina laminata*. Scale bar: 5 mm (whole specimens); 2.5 mm (details).

black specimens of *Limax* Linnaeus, 1758 was found in different stations, also in sympatry with *L. cf. maximus* (Fig. 9). A further *Limax* species with uniform brown colour was recorded.

A small black specimen of *Deroceras* Rafinesque, 1820 was collected in Stn. 8, externally resembling *Deroceras lothari*, a species described as endemic to Reatini Mountains (northern Latium) (Giusti, 1973). It is provisionally reported as *Deroceras cf. lothari* pending further study.

Holm oak and mixed woods are poorer in terms of both species and number of specimens. Pastures show a relatively reduced number of species as well, some of which deserve some comments. *Jaminia quadridens* occurs in two distinct forms, here referred to as small and large morphotype, respectively (Figs. 4, 5, 19, 20). At a conchological level, they mainly differ with regard to shell size. Measurements on over 60 specimens show that these two forms can be readily distinguished by the shell width, which shows a clear gap between the two morphotypes (Fig. 25). Moreover, the large morphotype seems to show a proportionally larger width. However, this feature needs confirmation due to the small amount of recorded specimens of

the small morphotype. The large morphotype is widespread and was recorded from several stations. Conversely, the small morphotype is uncommon and was recorded only at higher altitudes. A similar scenario with different morphs of *J. quadridens* occurring syntopically have been recorded also in other localities of Central Apennines, often with the occurrence of an additional, dextral morph.

*Monacha campanica*, which we regard as a distinct species, is found throughout the Liri Valley up to high altitude. The genitalia of *M. campanica* are characterized by a very short penis provided with a large penial papilla and a slender epiphallus. The flagellum is as long as the epiphallus. The bursa copulatrix shows a thick duct, widened at the base. Specimens from Lepini Mountains share the same anatomy but show a rather different shell. In fact, they are smaller (max. diam. 16 mm) and lighter than those described by the marquis Paulucci (1881) (max. diam. 21 mm). Moreover, they show a less depressed spire and a narrower umbilicus. As a consequence, they are reported in Table 2 as *Monacha cf. campanica*, pending further study.

In Stn. 9 (Bassiano, road to Semprevisa, near the spring) an empty shell clearly different from

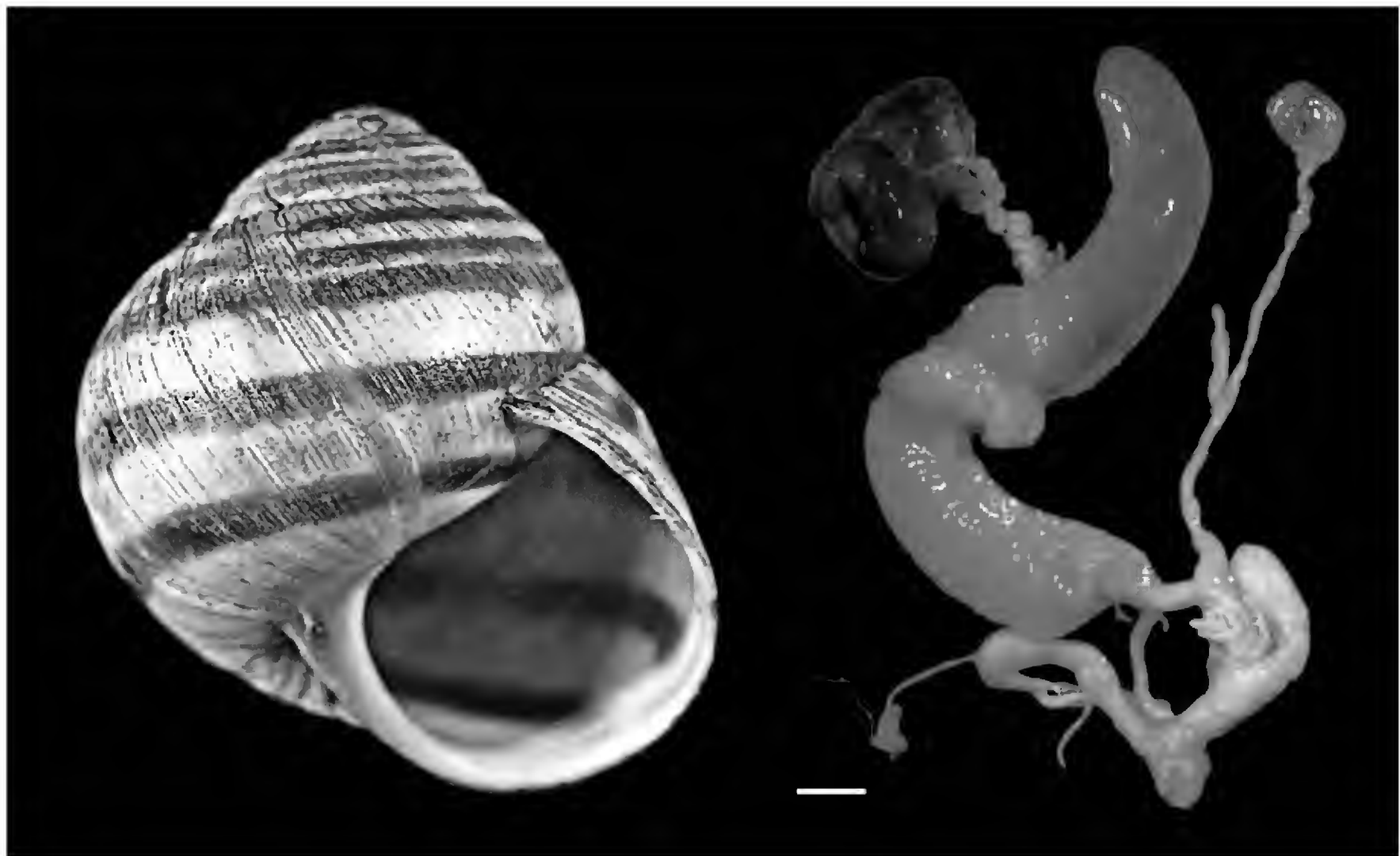


Figure 24. *Helix ligata*, height 35 mm, with genitalia (scale bar: 5 mm).



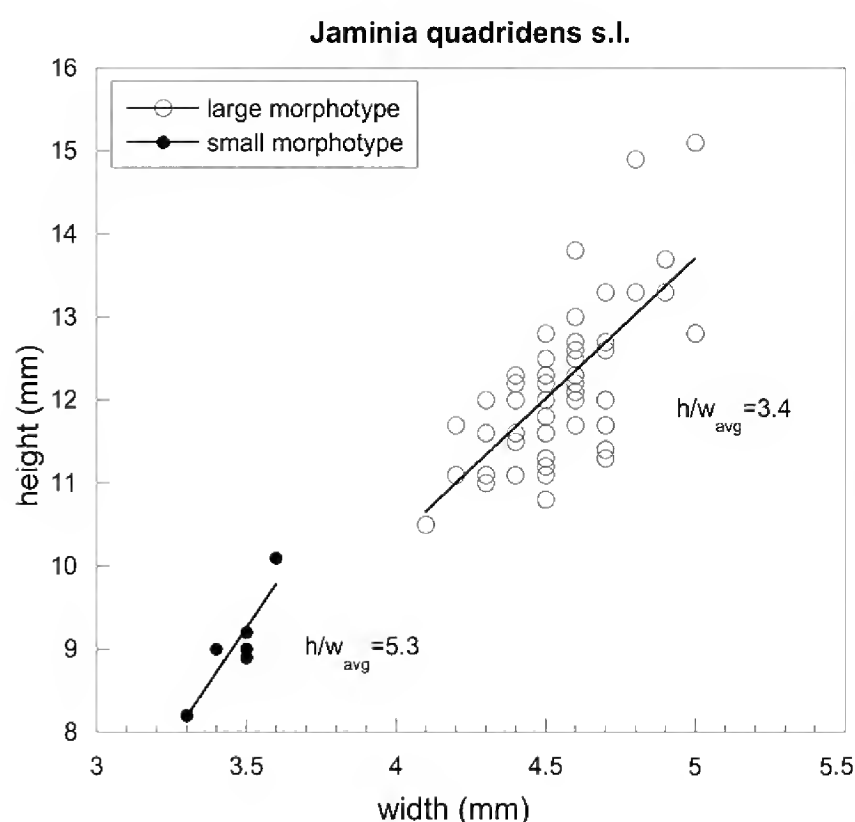


Fig. 25. Height and width measurements of *Jaminia quadridens* s.l. specimens from Lepini Mountains. Best-fit lines for the two morphotypes are shown.

*Monaca* cf. *campanica* has been collected. It is provisionally reported as *Monacha* cf. *cantiana* waiting for anatomical data.

*Ceruellopsis ghisottii* is the most abundant species in grasslands and pastures above 1000 m. This species shows a disjunct distribution in the Apennines. Southern populations occur in the Pollino (Calabria-Basilicata) and Sirino (Basilicata) massifs and extend up to Alburni Mountains (Campania), whereas populations from Central Apennines are frequent on the western coastal chains and extend up to Simbruini Mountains (Latium). The species was never recorded from intermediate mountains of central-northern Campania.

*Helix ligata* is widespread in Lepini Mountains but never abundant. Different populations show a variable appearance. Specimens from Carpinetana Valley were genetically studied by Fiorentino et al. (2016) and are very similar to specimens from Apennine valley floors showing a yellowish background due to the presence of periostracum, whereas specimens from Stn. 1 (pass to Campo di Segni) living in exposed pasture with stones show a whitish background (Fig. 24) likely due to the loss of periostracum that make it resemble *Helix delpretiana* Paulucci, 1878 (Giusti, 1973). However, the anatomy of specimens from Stn. 1 corresponds to

*Helix ligata*, even though they are genetically distinct from populations from Central Apennines (Fiorentino et al., 2016).

## CONCLUSIONS

The preliminary checklist here presented shows that at least 43 species of terrestrial gastropods occur in the Lepini Mountains. The richest environment is represented by beech forests, with 28 recorded species. Along with species already reported from Central Apennines, a new isolated population of *Medora* is recorded. Due to the extremely limited distribution, this population can be considered vulnerable and likely in need of protection. *Jaminia quadridens* occurs in two clearly distinct morphs without intermediate forms, mainly differing in their size. Further research is required in order to ascertain whether they actually belong to different species. Some species remain undetermined, whereas others were determined by comparison, pending further research.

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# A revision of the Mediterranean Raphitomidae, 3: on the *Raphitoma pupoides* (Monterosato, 1884) complex, with the description of a new species (Mollusca Gastropoda)

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## ABSTRACT

In the present work we present a complex of species of the family Raphitomidae (Mollusca Gastropoda) comprising three entities: two have multispiral protoconchs, *Raphitoma pupoides* (Monterosato, 1884), the less known *R. radula* (Monterosato, 1884) and a new species with paucispiral protoconch.

## KEY WORDS

Mollusca; Conoidea; Raphitomidae; new species; Mediterranean Sea.

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## INTRODUCTION

The family of Raphitomidae is a well supported clade of the Conoidea (Bouchet et al., 2011). The genus *Raphitoma* Bellardi, 1847 as currently conceived includes, based on our estimates, ca. 40 Mediterranean species, some of which are still undescribed. Propaedeutic to the general revision of the Mediterranean *Raphitoma* s.l., we have focused on several pairs of species, differing only or mostly in the size and shape of the protoconch (Pusateri et al., 2012, 2013). The specific distinction is based on the assumption that the dichotomy multispiral protoconch/planktotrophic development vs. paucispiral protoconch/lecithotrophic development (Jablonski & Lutz, 1980) can be used in caenogastropods to recognise distinct sister species (Bouchet, 1989; Oliverio, 1996a, 1996b, 1997). Anyway, it should not be abused to create polyphyletic genera by artificially separating closely

related species among different genera only based on their larval development (Bouchet, 1990).

In the present work we present the results on a complex of species comprising three entities: two have multispiral protoconchs, *R. pupoides* (Monterosato, 1884), and the less known *R. radula* (Monterosato, 1884); the other was discovered while revising the materials in the Monterosato collection, where a lot (MCZR 16905) included some specimens with paucispiral protoconch, labelled by Monterosato himself “*V. tomentosa/Monts./Palermo*”, never published, that we describe hereby as new to Science.

ABBREVIATIONS AND ACRONYMS. d = diameter; h = height; sh = empty shell(s); LMG-NS: Leeds Museums and Galleries - Natural Science; MNHN: Musée Nationale Histoire Naturelle, Paris, France; MRSNT: Museo Regionale Storia Naturale, Terrasini, Italy; NMW: National Museum of Wales, United Kingdom; SMF: Senckenberg Museum,

Frankfurt/M, Germany; SMNH: Swedish Museum of Natural History, Stockholm, Sweden; MCZR: Museo Civico di Zoologia, Roma, Italy; HUJ: Hebrew University of Jerusalem, Israel; ARD: Roberto Ardevini collection (Rome, Italy); BOG: Cesare Bogi collection (Livorno, Italy); DUR: Sergio Duraccio collection (Napoli, Italy); GER: Alfio Germanà collection (Trecastagni, Catania, Italy); GOR: Sandro Gori collection (Livorno, Italy); HOA: André Hoarau collection (Fréjus, France); MAC: Gabriele Macrì collection (Scorano, Lecce, Italy); MAR: Alessandro Margelli collection (Livorno, Italy); PAG: Attilio Pagli collection (Lari, Pisa, Italy); PAO: Paolo Paolini collection (Livorno, Italy); PRK: Jakov Prkić collection (Split, Croatia); PSI: Peter Sossi collection (Trieste, Italy); PUS: Francesco Pusateri collection (Palermo, Italy); SBR: Carlo Sbrana collection (Livorno, Italy); SER: Gabriele Sercia collection (Palermo, Italy); SPA: Gianni Spada collection (Vagrigneuse, France); SQU: Ennio Squizzato collection (Loreggia, Padova, Italy); TIS: Morena Tisselli collection (S. Zaccaria, Ravenna, Italy); TRI: Lionello Tringali collection (Rome, Italy); VAZ: Angelo Vazzana collection (Reggio Calabria, Italy).

## RESULTS

### *Systematic*

Citation of unpublished names is not intended for taxonomic purposes.

Familia RAPHITOMIDAE Bellardi, 1875

Genus *Raphitoma* Bellardi, 1847

Type species: *Pleurotoma hystrix* Cristofori et Jan, 1832 (nomen nudum, validated by Bellardi, 1847 as "*Pleurotoma hystrix* Jan.") by subsequent designation (Monterosato, 1872: 54).

***Raphitoma pupoides*** (Monterosato, 1884)

Figs. 1–9, 24

*Pleurotoma rudis* Scacchi, 1836 non G.B. Sowerby I, 1834 nec Philippi, 1836

*Pleurotoma rudis* Scacchi, Weinkauff, 1868: 130 (see Remarks)

*Pleurotoma reticulatum* var. *rudis* Sc., Petit de la Saussaye, 1869: 154

*Pleurotoma (Defrancia) rudis* Sc., Monterosato, 1875: 44 (see Remarks)

*Pleur. rude* Scacchi, Aradas & Benoit, 1876: 249 n. 662 (see Remarks)

*Pleurotoma rudis* Sc., Monterosato, 1878: 106 (see Remarks)

*Clathurella rudis* Scacchi, B.D.D., 1883: 94 pl. 14 figs. 8, 9

*Cordieria pupoides* Monterosato, 1884: 132 [nomen novum]

*Clathurella pupoidea* Monterosato, Locard, 1886: 114 [error pro *pupoides*]

*Clathurella pupoidea* Monterosato, Locard, 1891: 66 fig. 52 [error pro *pupoides*]

*Clathurella rudis* (B.D.D.), Carus, 1893: 426

*Clathurella pupoidea* de Monterosato, Locard & Caziot, 1900: 248

*Clathurella pupoidea* var. *major*, Locard & Caziot, 1900: 248 (nomen nudum)

*Clathurella pupoidea* var. *minor*, Locard & Caziot, 1900: 248 (nomen nudum)

*Clathurella pupoidea* var. *ventricosa*, Locard & Caziot, 1900: 248 (nomen nudum)

*Clathurella pupoidea* var. *curta*, Locard & Caziot, 1900: 248 (nomen nudum)

*Clathurella pupoidea* Mtrs., Kobelt, 1905: 351

*Mangilia (Clathurella) pupoides* Monterosato, Cipolla, 1914: 146, pl. 13, figs. 16 (fossil)-17 (recent)

*Cordieria pupoides* Montrs., Bellini, 1929: 32

*Philbertia (Philbertia) rudis* Scacchi, Priolo, 1967: 697

*Raphitoma (Cyrtoidea) rudis* (Scacchi), Nordsieck, 1968: 176 pl. 30, fig. 20

*Raphitoma (Cyrtoidea) rudis pupoidea* (Monterosato), Nordsieck, 1968: 176 pl. 30 fig. 21

*Raphitoma rudis pupoidea* Monts, Parenzan, 1970: 207 pl. 44, fig. 842

*Raphitoma (C.) pupoidea* (Monterosato), Nordsieck, 1977: 52, pl. 16, fig. 126 (error pro *pupoides*)

*Raphitoma (C.) neapolitana* Nordsieck, 1977: 52, pl. 16 figs. 124, 125 (nomen vanum)

*Raphitoma pupoides* (Mts), Terreni, 1981: 40 n. 328

*Raphitoma pupoidea* (Monterosato), Nordsieck, 1982: 272, pl. 101, fig. 98.11

*Raphitoma neapolitana* Nordsieck, 1982: 272, pl. 101, fig. 98.10

*Raphitoma neapolitana* form *a* Nordsieck, 1982: 272, pl. 101, fig. 98.10a

- Raphitoma* (*R.*) *pupoides* (Monterosato), Van Aartsen et al., 1984: 91
- Raphitoma pupoides* (Monterosato), Orlando & Palazzi, 1986: 44
- Raphitoma pupoides* (Monterosato), Tenekidis, 1989: n. 58.50
- Raphitoma* (*Raphitoma*) *pupoides* (Monterosato), Sabelli et al., 1990–1992: 44, 216, 411
- Raphitoma pupoides* (Monterosato), Poppe & Goto, 1991: 174
- Raphitoma* (*Cyrtoides*) *pupoides* (Monterosato), Delamotte & Vardala-Theodorou, 1994: 287
- Raphitoma pupoides* (Monterosato), Cecalupo & Quadri, 1995: 109
- Raphitoma pupoides* (Monterosato), Giribet & Peñas, 1997: 53
- Raphitoma pupoides* (Monterosato), Marquet, 1998: 276
- Raphitoma pupoides* (Monterosato), Oztürk et al., 2004: 59
- Raphitoma pupoides* (Monterosato), Repetto et al., 2005: 220 fig. 910
- Pleurotoma rudis* Scacchi, Cretella et al., 2005: 125
- Raphitoma pupoides* (Monterosato), Cretella et al., 2005: 125
- Raphitoma pupoides* (Monterosato), Cossignani & Ardovini, 2011: 31, 328
- Raphitoma pupoides* (Monterosato, 1884), Scuderi & Terlizzi, 2012 (see Remarks)

TYPE LOCALITY. Coast of Provence, France, Mediterranean Sea.

EXAMINED MATERIAL. Type material: neotype, from “Artufel/Provenza” [Provence, M. Artufel legit] (18.7 x 7.7 mm) (MCZR 16492).

OTHER EXAMINED MATERIAL. France. “Artufel/Provenza” 3 sh (MCZR 16492, with Monts label “*H. pupoides*”); Marseille, 4 sh (coll. Locard MNHN); St. Raphael, 3 sh coll. Locard (MNHN), 1 sh (coll. Hoarau); Cassis, 2 sh coll. (Locard MNHN); Le Brusc, 4 sh (coll. Locard MNHN, 4 sh); Coste di Provenza, 2 sh (coll. Chaster NMW n. 01894); Bastia, 2 sh (coll. Monterosato, MCZR lot 16861).

Italy. Gulf of Baratti, 7 sh (PAO), 1 sh (PAG); Punta Ripalti (Elba Isl.), 2 sh -25 m (GOR); Lazio 1 sh (PAG); Circeo, 1 sh (TRI); Napoli, 1 sh (coll. Coen HUIJ, n. 8082c sub nomine “*Philbertia* (*Cordieria*) *cordieri cancellata*”); Sorrento

(Napoli), 2 sh (DUR); Palinuro (Salerno), 1 sh (SPA); Scilla (Reggio Calabria), 4 sh (VAZ); Palermo, Sicily, 10 sh with Monterosato handwritten label “*pupoides*/Monts./Pal!!/et/v. *decolorata*, Pallary”, 1 sh with non-Monterosato label “*Cordieria/pupoides* Monts./dr. Golfo di Palermo” and 15 sh with non-Monterosato label “*Cordieria/pupoides* Monts./drag. Golfo di Palermo” (MCZR 16492, with Monts label “*H. pupoides*”); Porticello (Palermo), 2 sh sub nomine *R. reticulata* (coll. MRSNT n. 4759); Isola delle Femmine (Palermo), 1 sh (SER), 8 sh (PUS); Trapani, 1 sh (SER); Catania, 1 sh (GER); Pozzillo Inferiore (Catania), 1 sh (PAG); Canale di Sicilia, 1 sh (TRI), 1 sh (coll. MRSNT n. 7312); Sicilia, 6 sh sub nomine *R. purpurea* (coll. MRSNT n. 29824); Jesolo (Venezia), 1 sh (SQU).

“Coste d’Africa”. 1 sh, coll. Monterosato MCZR, lot 16901.

Croatia. Unprecised locality, 1 sh (DEL); Dalmatia, 1 sh (PRK).

DESCRIPTION. In squared parentheses data of the neotype. Shell of medium size for the genus, height 10–21 mm [18.7] (mean 15.05, std 3.81), width 5–8 mm [7.7] (mean 6.57, std 1.27), cirto-pupoid, slender, h/d 2.1–2.57 [2.43] (mean 2.26, std 0.19). Protoconch multispiral, only part of the last whorl known, with traces of diagonally cancellate sculpture. Teleoconch of 6–8 [7] whorls, evenly convex (more convex in juveniles). Suture fine and undulate. Axial sculpture of 12–24 [18] slightly opisthoclinal, non-equidistant ribs, and interspaces broader than the ribs (with interspace width varying with shell size). Axial sculpture evident, but becoming obsolescent in largest shells. In particularly large shells (gerontic), axial ribs revert to same strength as the spiral cords on the last quarter of whorl. Spiral sculpture on the last whorl of 7–10 [9] cordlets, thinner than axial ribs. Cancellation squared in juveniles, becoming rectangular in adults. Secondary cordlets appearing occasionally and thereafter becoming as strong as the others. Subsutural ramp narrow, devoid of evident sculpture. Columella simple, slightly sinuous anteriorly, gently angled posteriorly. Outer lip thickened and crenulated externally, with 11–13 [12] strong inner denticles, the most posterior smaller, delimiting the wide and short anal sinus, the most anterior more robust and delimiting the funnel-like siphonal canal. Siphonal fasciole of 6 nodulose cordlets, neatly spaced from the last spiral cordlet. Colour uniformly light chestnut brown in the back-



ground, with darker blotches, more evident in larger shells (>20 mm), and same darker colour bordering the siphonal fasciole and inside the aperture. Violet hue on the first 3–4 whorls of particularly fresh specimens. Comma-shaped white spots on the sub-sutural ramp, arrow-like white spots inside some cancellation interspaces. Soft parts unknown.

**DISTRIBUTION.** Western and Central Mediterranean. Adriatic. The records under this name from Greece by Koukouras (2010) and Delamotte & Vardala-Theodorou (1994: 287) were in turn based on Tenekides (1989) who reported under this name another species (probably *R. echinata*).

**REMARKS.** The protoconch was always either lacking, broken or corroded in almost specimens studied. Anyway parts of the apical whorls showing traces of a diagonally cancellate sculpture, indicating a multispiral protoconch.

*Pleurotoma rudis* Scacchi, 1836 was introduced with the following diagnosis: “*Testa fusca fascis pallidioribus, anfractibus rotundatis, cancellatis et muricatis; labro crasso interne striato, cauda vix ultra labrum producta. Alta lin. 10–11. P. echinatae similis; at labro crassiore, cauda brevior, et minus aspera; saepe fascis pallidioribus ornata. In sinu neapolitano et tarentino*” (Scacchi, 1836), Fig. 17.

Weinkauff (1868), Petit de la Saussaye (1869) and Aradas & Benoit (1876) considered it as a variety or synonym of *R. echinata* (as *Defrancia reticulata* Renier). Monterosato (1875, 1878) at first included it within *Pleurotoma purpurea* sensu Philippi non Montagu. Thereafter (Monterosato, 1884), he separated to two species and introduced the replacement name *Cordieria pupoides* noticing an alleged homonymy with “*P. rudis* Broderip”. Actually, Broderip introduced, in 1834, *Placunanomia rudis* (a bivalve), the abbreviation *P. rudis* having possibly mislead Monterosato. However, *Pleurotoma rudis* Scacchi is preoccupied by *P. rudis* G.B. Sowerby I, 1834 (currently accepted as *Crassispira rudis*) and by *P. rudis* Philippi, 1836 (currently accepted as *Clathromangelia granum* (Philippi, 1844): note that Philippi’s work preceeds Scacchi’s one according to Cretella et al., 2005: 115), and the replacement name by Monterosato still holds valid. Regrettably, the type material of *Pleurotoma rudis* Scacchi is lost (Cretella et al., 2005: 123) and we have established hereby a neotype based on Monterosato’s material. The original material of

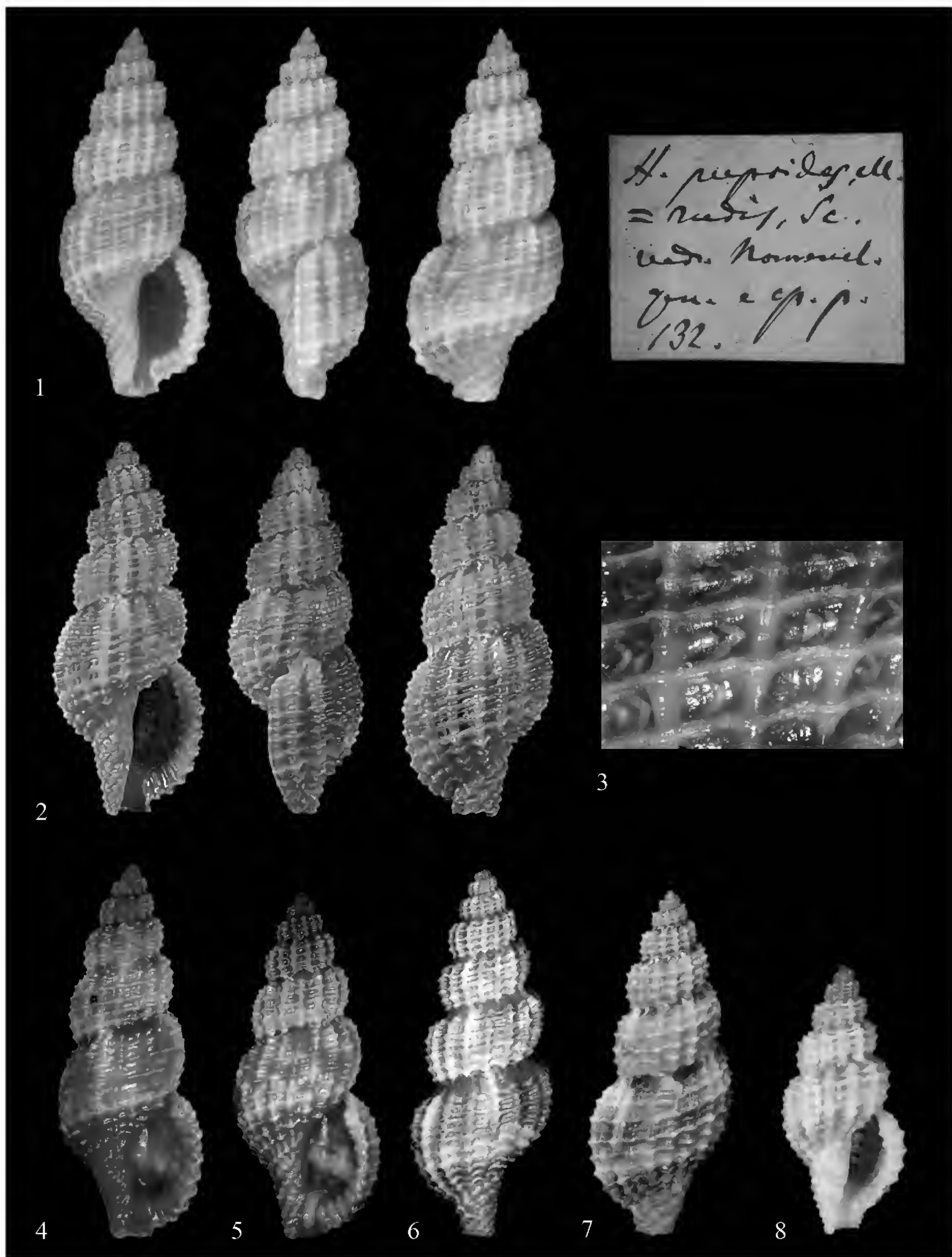
*Pleurotoma rudis* Scacchi has gone lost. We designate, for the sake of stability, a shell from the Monterosato collection, upon which he based his concept of *Cordieria pupoides*, as the neotype of *Pleurotoma rudis* Scacchi.

Some Authors (Bucquoy et al., 1883: 93) included, in the synonymy of *R. rudis*, *Pleurotoma reticulata* var. *brevis* Requi  n, 1848. However, this is a nomen nudum and thus, not available. Nordsieck (1977) used this name (*brevis*) and provided the first valid introduction, but referring to a distinct species.

Nordsieck (1968: 176) split *R. rudis* Scacchi into four subspecies: *R. rudis rudis*, *R. rudis pupoidea* [sic!], *R. rudis cylindrica* and *R. rudis intermedia*. Descriptions of *R. rudis rudis* and *R. rudis pupoidea* [sic! error pro *pupoides*] are quite similar and might be referred to the same species (*R. pupoides*). Concerning the two other “subspecies”, *R. cylindrica* (erroneously ascribed to Monterosato, actually introduced by Locard & Cazi  t, 1899) is a distinct unrelated species; “*R. rudis intermedia* n. ssp.” had a scanty description and was not figured. Subsequently, Nordsieck raised it to species level and provided a description and figure of *R. intermedia* (Nordsieck, 1977: 56, pl. 18 fig. 140). This is *R. laviae*, as confirmed by the study of a syntype (SMF, sine numero, with autograph Nordsieck’s label). To increase confusion, Nordsieck (1977: 52) also introduced *R. (Cyrtoides) neapolitana* as a replacement name pro *Pleurotoma rudis* Scacchi, 1836 non Broderip, evidently neglecting Monterosato’s introduction: *R. neapolitana* is thus not available. Material on which Nordsieck based his concept of *R. neapolitana* (SMF 340337, 3403379 and 340338) included small size specimens of *R. laviae* and *R. bicolor*.

*Raphitoma* cfr. *pupoides* as figured by Cavallo & Repetto (1992: 147 fig. 401) and *R. cfr. pupoides* as figured by Cachia et al. (2001: 69 pl. 10 fig. 9) are not referable to the present species. *Raphitoma pupoides* as figured by Scuderi & Terlizzi (2012: pl. XVIII n. 6) is rather to be referred to *R. cordieri* sensu Auctores.

*Raphitoma pupoides* can be easily distinguished from *R. echinata* sensu Auctores by its cyrtconoid not stepped outline and the shorter siphonal canal. Specimens of *R. pupoides* with strong sculpture on the last whorls may be confused with *R. radula*, which is however diagnosed by its more acute spire, the lighter colour without blotches or spots.



Figures 1–8. Shells of *Raphitoma pupoides* (Monterosato, 1884). Fig. 1: Lectotype: Provenza, (MCZR lotto 16492), h: 18.7 mm with label of the lot; Fig. 2: sine locus (MNHN-IM-2000-3240), h: 16.5 mm; Fig. 3: Palinuro, close-up of the sculpture; Fig. 4: Anzio, h: 20 mm; Fig. 5: Anzio, h: 17 mm; Fig. 6: Jesolo (Venezia), h: 20 mm; Fig. 7: Saint-Raphael, Est La Chrétienne (France), h: 15.7; Fig. 8: Isola delle Femmine (Palermo), juveniles, h: 9.1 mm.

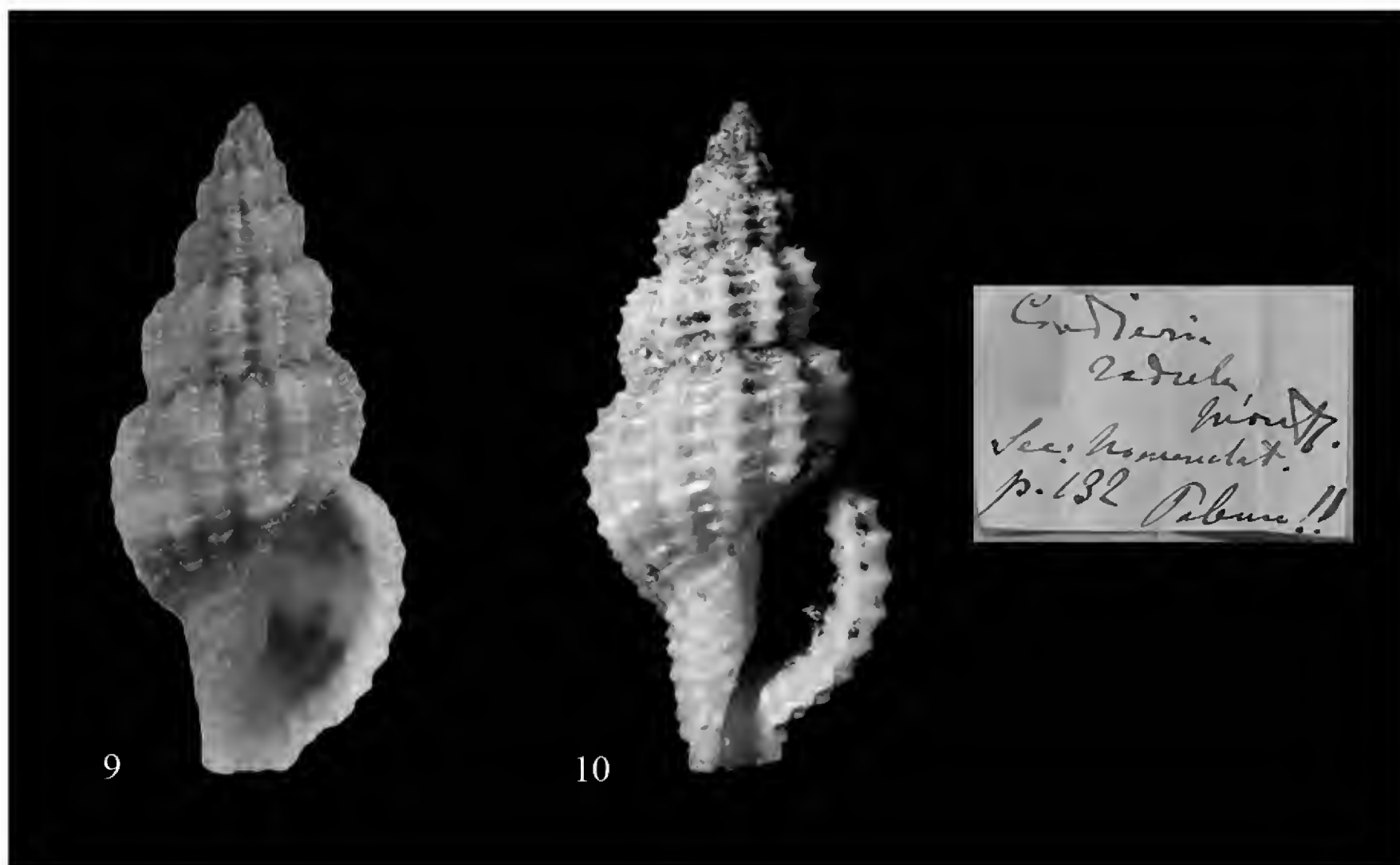


Figure 9. *Raphitoma pupoides* (Monterosato, 1884), Adriatic, h: 12 mm.

Figure 10. *Raphitoma radula* (Monterosato, 1884), Palermo, coll. Melville-Tomlin, NMW, h: 11.5 mm, with label.

***Raphitoma alida*** Pusateri et Giannuzzi-Savelli  
n. sp. - Figs. 11–15, 25

EXAMINED MATERIAL. Holotype and 3 paratypes from Palermo (coll. Monterosato, MCZR 16905), with handwritten Monterosato label: "*V. tomentosa*/Monts./Palermo"; 2 paratypes, Gulf of Palermo (PUS).

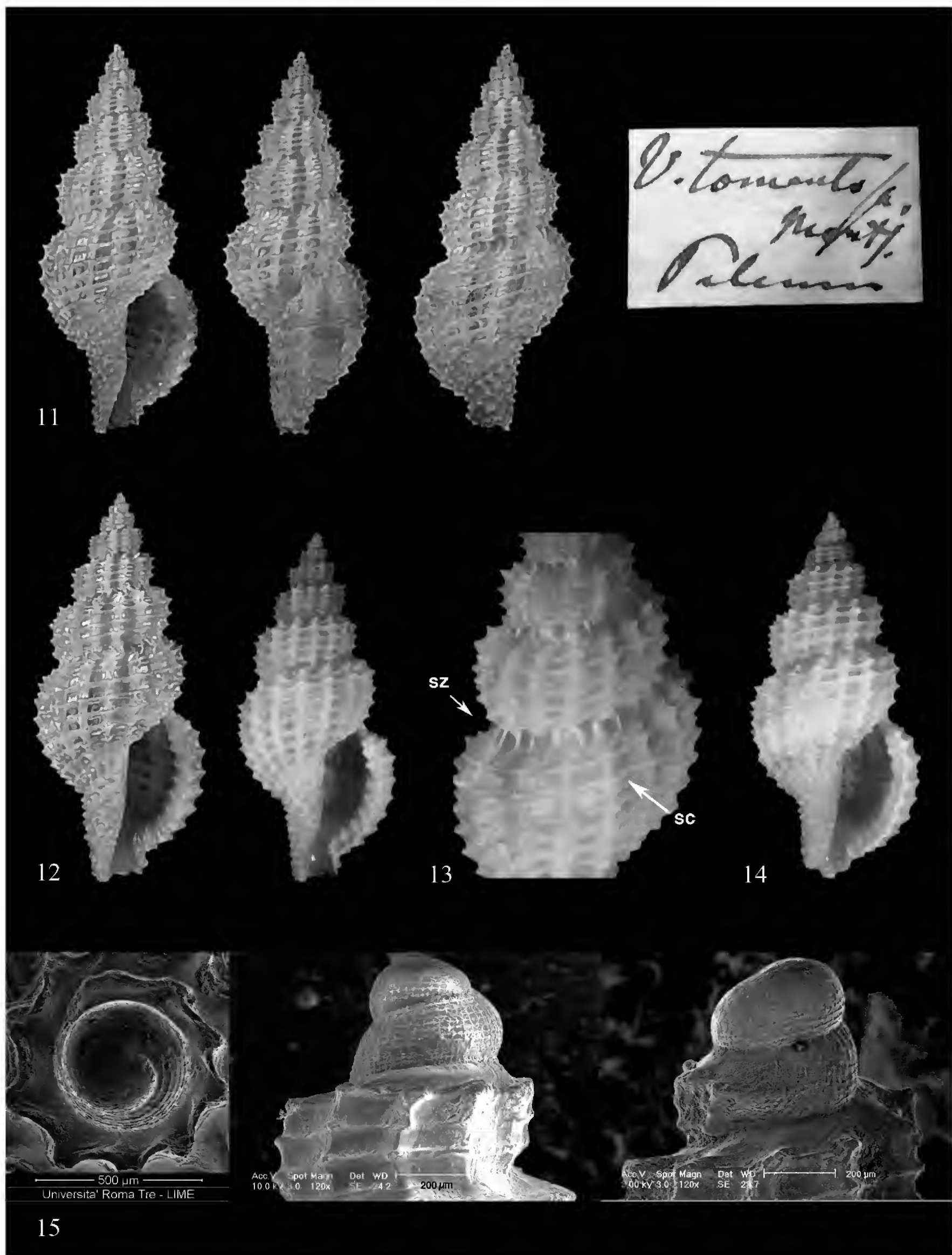
OTHER EXAMINED MATERIAL. Italy. Gulf of Baratti, 1 sh (MAR), 1 sh (BOG); Livorno, 1 sh (BOG); Scilla (Reggio Calabria), 3 sh (VAZ); Palermo, 1 sh sub nomine ms. "*perfecta*" (coll. Monterosato, 16905); sine loco probably Palermo, 1 sh, (coll. Monterosato, MCZR 16905); Gulf of Palermo, 2 sh (PUS).

"Coste d'Africa". 1 sh (coll. Monterosato, MCZR 16905).

DESCRIPTION OF HOLOTYPE. Shell of medium size for the genus, height 17.1 mm, width 7 mm, fusi-form-pupoid, slender, h/d 2.44 mm. Protoconch paucispiral, only protoconch I of 1.5 convex whorls, height 540  $\mu$ m, width 480  $\mu$ m; sculpture orthogonally cancellate. Teleoconch of 7 convex whorls. Suture not incised, evident. Axial sculpture

of 16 slightly opisthocline (sometimes orthocline), elevated and strong ribs, and interspaces twice as broad as the ribs. Spiral sculpture on the last whorl of 6 cordlets, thinner than axial ribs and interspaces twice as broad as the cordlets. Cancellation rectangular, with spinulose tubercles at the intersections. Secondary cordlets appearing occasionally and thereafter becoming as strong as the others. Subsutural ramp wide, devoid of evident sculpture. Columella simple, slightly sinuous anteriorly, gently angled posteriorly. Outer lip thickened and crenulated externally, with 9 strong inner denticles, the most posterior smaller, delimiting the wide and deep anal sinus, the most anterior more robust and delimiting the funnel-like siphonal canal. Siphonal fasciole of 7 nodulose cordlets, neatly spaced from the last spiral cordlet. Colour straw yellow, becoming gradually orange-brownish in the subsutural area, and with an orange-brown band visible inside the aperture. Comma-shaped white spots on the subsutural ramp, arrow-like white spots inside some cancellation interspaces. Soft parts are unknown.

VARIABILITY. Paratypes shells: height 12–17 mm (mean 14.4, std 1.66), width 5.5–7 mm (mean 6.36,



Figures 11–14. Shells of *Raphitoma alida* n. sp. Fig. 11: Holotype, Palermo (coll. Monterosato MCZ, lot 16905), h: 17.1 mm; Fig. 12: Paratype A, Palermo (coll. Monterosato MCZR, lot 16905), h: 14.8 mm; Fig. 13: Paratype E, Gulf of Palermo, (PUS n. 405), h: 12.1 mm (sz = subsutural zone; sc = secondary cordlet); Fig. 14: Gulf of Palermo, h: 12.8 mm. Figure 15. *Raphitoma alida* n.sp., protoconch of the holotype.



std 0.57), h/d 2.12–2.36 mm (mean 2.26, std 0.10); axial sculpture of 14–16 ribs; outer lip with 9–10 denticles. Soft parts are unknown.

ETYMOLOGY. From the two granddaughters of the authors (Alice Giannuzzi Savelli and Ida Pusateri), ali[ce]+ida, used as a noun in apposition.

DISTRIBUTION. This new species is known only for the examined material, from Tyrrhenian and Central Mediterranean. Type locality is Palermo.

REMARKS. *Raphitoma alida* n. sp. differ from *R. pupoides* mainly in its paucispiral protoconch (v. multispiral in *R. pupoides*). Shells without protoconch of the new species could be confused with shells of *R. pupoides* with a non-obsolete sculpture on the last whorl; *R. alida* n. sp. can be distinguished by its different background colour (chestnut v. yellowish), 7 nodulose cordlet on the fasciole v. 6 less nodulose in *R. pupoides*, and the less pupoid and more fusiform outline.

Some recent Authors (Nordsieck, 1968, 1977; Piani, 1980) erroneously ascribed to Monterosato a validly published “*Raphitoma tomentosa*”. Although the epithet “*tomentosa*” was evidently especially liked by Monterosato, he has never published such binomen. The epithet “*tomentosa*” was, for mysterious reasons, to be particularly dear and pleasing to Monterosato so that in schedis, gave this name to various entities: - *Philbertia tomentosa*, lot 16682 = some mixed specimens of *R. philberti* var. - *D. tomentosa*, lotto 16901 = 4 specimens of *R. horrida*. - *P. tomentosa* lotto 16696 = 5 specimens of *R. lineolata*. - *Philbertia tomentosa*, Monterosato’s label in coll Coen lot 1912 = 2 specimens of *R. pruinosa*.

Nordsieck (1968: 177) reported *Raphitoma philberti tomentosa* with a useless scanty description (“*kleiner, gedrungen mit konvexen Umgangen. Schlanker stiel. Hell reh-weiss*”; small, stout, with convex whorls. Slender tail. Light fawn and white) and without any figure. Nordsieck (1977: 58 n. A149) again reported *Raphitoma (Philbertia) tomentosa* ascribing it to Monterosato, 1884, with an apparently good description and a figure (Nordsieck, 1977: pls. 19 n. 149). However, the four lots labelled under this name in the coll. Nordsieck included the following materials:

SMF 341803/1, labelled “*Philbertia tomentosa* Mtrs. Egina”, one worn shell, 5.4 mm long, with two holes, protoconch missing, probably *R. laviae*;

SMF 341804/1, labelled “*Philbertia tomentosa* Mtrs. Karpathos”, one very worn shell, 3.2 mm long, protoconch missing, probably *R. bicolor* juv.; SMF 341805/1, labelled “*Philbertia tomentosa* Mtrs, Cataldo (Brindisi)”, one very worn shell, 5.9 mm long, protoroch missing, indeterminable. Nordsieck (1977: 58) reported “Palermo, Cataldo”: although there is a beach called San Cataldo near Terrasini (Palermo), it is more likely that the true locality was San Cataldo, not far from Brindisi; SMF 341802/5, labelled as “*Philbertia tomentosa* Mtrs., Ibiza”, 5 shells, 2.5–6.5 mm long, four too worn to be identified, one referable to *R. bicolor* juv., with a portion of multispiral protoconch.

None of these shells matched the description, the size (7 x 3.2 mm) or the figure provided by Nordsieck, including the described paucispiral protoconch, whilst all but one shells (with traces of multispiral protoconch) lacked the apex. It is worthy of notice that Nordsieck’s “descriptions” were not necessarily based (only) on actual specimens but frequently included also a compilation from literature. Same holds for his drawings, often compound artwork of actual specimens and figures from the literature. This explains why so rarely specimens can be found which match his figures (our unpublished observations and R. Janssen, SMF, personal communication). Nordsieck included this entity in the subgenus *Philbertia*, which in his scheme comprised species (*R. philberti*, *R. laviae*, *R. lineolata*, *R. atropurpurea*, *R. densa*, etc.) that have nothing to do with the *R. pupoides*-complex. Parenzan (1970: 212 n. 862) cited *R. philberti* var. *tomentosa* Monterosato evidently mutuating it after Nordsieck (1968). This name is anyway unavailable, having been introduced as a varietal name after 1960 (ICZN, 1999: art. 15.2).

***Raphitoma radula*** (Monterosato, 1884) [*Cordieria*]  
Figs. 10, 16–23, 26

*Cordieria radula* Monterosato, 1884: 132

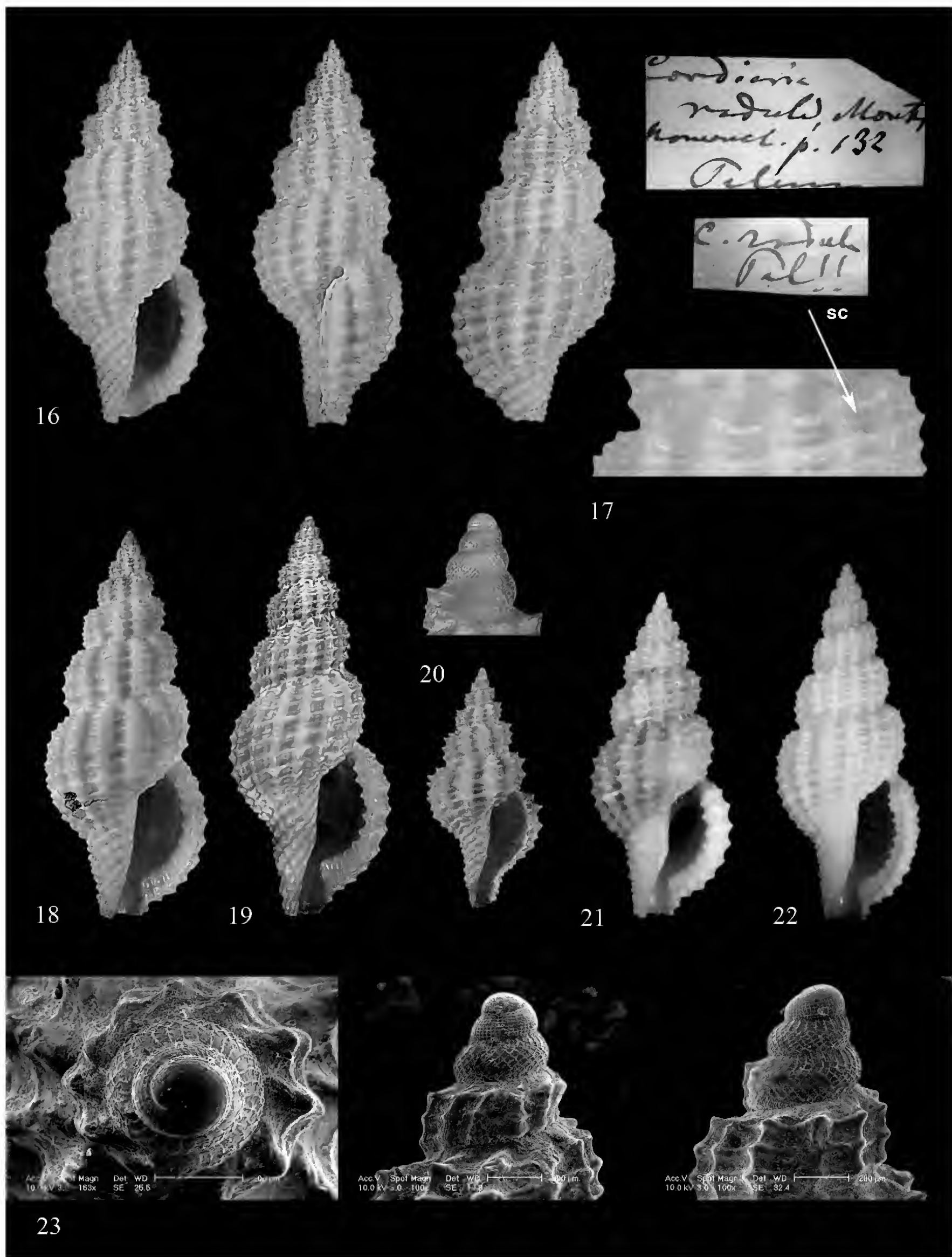
*Clathurella radula* de Monterosato, Locard, 1886: 117

*Clathurella radula* de Monterosato, Locard, 1891: 67

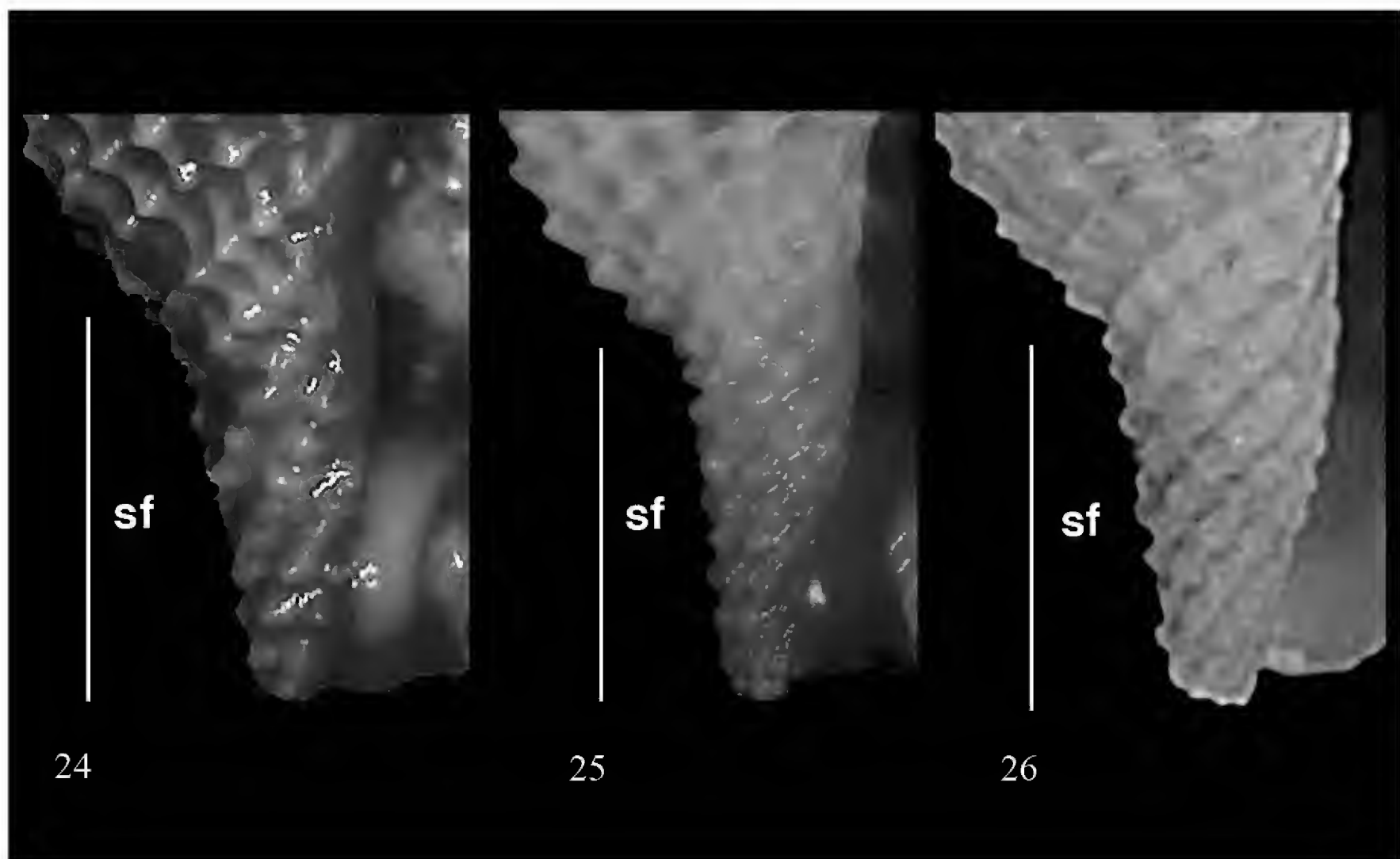
*Clathurella radula* de Monterosato, Locard & Caziot, 1899: 250

*Clathurella radula* var. *elongata*, Locard & Caziot, 1899: 250 (nomen nudum)





Figures 16–22. Shells of *Raphitoma radula* (Monterosato, 1884). Fig. 16: Lectotype, Palermo, (MCZR), h: 14.8 mm; Fig. 17: particular (sc = secondary cordlet); Fig. 18: Palermo (coll. Monterosato MCZR), Paralectotype A, h: 17 mm; Fig. 19: Isola d'Elba, h: 18 mm; Fig. 20: Palermo (coll. Monterosato MCZR), Paralectotype F, h: 6 mm; Fig. 21: Antignano (Livorno), h: 9.9 mm; Fig. 22: Gulf of Palermo, h: 12.7 mm. Figure 23. *Raphitoma radula*, protoconch of paralectotype F.



Figures 24–26. Siphonal fasciole of *Raphitoma pupoides* (Fig. 24), *R. alida* (Fig. 25), and *R. radula* (Fig. 26).

*Clathurella radula* var. *fuscescens*, Locard & Caziot, 1899: 250 (nomen nudum)

*Clathurella radula* var. *lutescens*, Locard & Caziot, 1899: 250 (nomen nudum)

*Clathurella radula* var. *minor*, Locard & Caziot, 1899: 250 (nomen nudum)

*Clathurella radula* var. *ventricosa*, Locard & Caziot, 1899: 250 (nomen nudum)

*Cordieria radula* Monterosato, Pallary, 1900: 256

*Raphitoma reticulata radula* Nordsieck, 1968: 175, pl. 29 fig. 94.16

*Raphitoma echinata cordieri* form d (radula) Monterosato, Nordsieck, 1977: 51

*Cordieria radula* (Monterosato), Sabelli et al., 1990: 217

TYPE LOCALITY. Palermo.

EXAMINED MATERIAL. Lectotype (here designated, 14.8 x 6.4 mm) Monterosato coll (MCZR 16476), with handwritten label by Monterosato “*Cordieria/radula*, Monts/Nomencl. p. 132/Palermo”; and 11 paralectotypes Monterosato coll (MCZR 16476) with handwritten label by Monterosato “*C. radula*/ Pal!!”. Spain. Alboran, -80 m, 1 sh, (SBR); Cadiz, 1 sh (MNHN).

France. St. Henry (Marseille), 4 sh (coll. Locard MNHN); Marseille, 5 sh (coll. Locard MNHN); Toulon, 1 sh (coll. Locard MNHN); St. Raphael, 1 sh (coll. Locard MNHN); Sète, 2 sh (coll. Locard MNHN).

Italy. Secca delle Vedove, -120/130 m, 2 sh (PAO); Castiglioncello (Livorno), 1 sh (MAR); Capraia Isl., 1 sh (BOG); Napoli, 2 sh (coll. Monterosato, MCZR, sine numero, sub nomine ms. var. *aspera*); Puolo (Napoli), 1 sh (DUR); Ischia Isl., 1 sh (TRI); Gulf of Palermo, 10 sh (PUS); Gulf of Palermo, 3 sh (coll. Monterosato, MCZR lot 16492, 3), 2 sh (coll. Monterosato, MCZR lot 17342); Porto di Palermo, 2 sh (coll. Monterosato, MCZR lot 16476); Palermo, 3 sh (coll. Melville-Tomlin, NMW); Mondello (Palermo), 1 sh (coll. Monterosato sine numero, sub nomine “*purpurea albina*”); Sciacca, 1 sh (coll. Monterosato, MCZR lot 16492); Catania, (coll. Monterosato ex Aradas, MCZR, lot 16476, 2 sh).

Algeria. Sine loco, 2 sh (coll. Monterosato, MCZR lot 16492); Orano, 1 sh (coll. Pallary MNHN).

Croatia. Between Pula and Lighthouse of Porer, 1 sh, legit W. Koers (SMNH lot 70484).

**DESCRIPTION.** In squared parentheses data of the lectotype. Shell of medium size for the genus, height 9–19 mm [14.8] (mean 13.81, std 2.90), width 4–8 mm [6.4] (mean 5.90, std 1.10), fusiform-pupoid, slender, h/d 2.2–2.5 [2.31] (mean 2.32, std 0.09). Protoconch multispiral of 2.7 convex whorls, height 580 µm, width 440 µm; protoconch I of 1.1 whorls, width 210 µm, with irregularly placed small tubercles and orthogonally cancellate sculpture; protoconch II of 1.6 whorls, with a diagonally cancellate sculpture. Teleoconch of 7–8 [7] convex whorls. Suture not impressed. Axial sculpture of 12–17 [16] slightly opisthocline, elevate, strong ribs, and interspaces as broad as the ribs (or slightly broader). Growth lines visible between the ribs on the last whorl. Spiral sculpture on the last whorl of 5–6 [5] cordlets above the aperture, thinner than axial ribs, with interspaces three times as broad as the cordlets, and a secondary cordlet bordering the subsutural ramp. Cancellation squared. Secondary cordlets appearing occasionally and thereafter becoming as strong as the others. Subsutural ramp narrow, devoid of evident sculpture. Columella simple, slightly sinuous anteriorly, gently angled posteriorly. Outer lip thickened and crenulated externally, with 8–9 [9] (rarely up to 11) strong inner denticles, the most posterior smaller, delimiting the wide and deep anal sinus, the most anterior more robust and delimiting the funnel-like siphonal canal. Siphonal fasciole of 7–8 [7] nodulose cordlets, neatly spaced from the last spiral cordlet. Colour from uniformly whitish to very light chestnut brown, with darker subsutural ramp and darker band on the lower part of the last whorl. Violet hue on the background in particularly fresh specimens. Comma-shaped white spots on the subsutural ramp, arrow-like white spots inside some cancellation interspaces. Soft parts are unknown.

**DISTRIBUTION.** Provence, Western Mediterranean and Tyrrhenian. A single record from neighbouring Atlantic (Cadiz).

**REMARKS.** *Raphitoma radula* could be confused with shells of *R. pupoides* with non-obsolescent sculpture, but it is easily diagnosed by its homogeneous light coloration with violet hue. It could be mixed with very light or albinistic shells of *R. echinata* (of similar size) from which it differs in the less elevate spirals, the shorter and more rounded aperture and the violet hue in fresh specimens.

Monterosato (1884: 132) introduced *Cordieria radula* for the erroneously identified *P. purpureum* sensu Philippi (non Mtg.), referring to the examen (ex typo) of a specimen provided by Philippi himself to Sylvanus Hanley. According to Clare Brown (Leeds Museum Discovery Centre) “Hanley’s collection came to us [LMG-NS] in the 1950s after being broken up and many parts sold on. Sadly, it seems as if the Philippi *P. purpurea* didn’t make it to Leeds”. However, there is little doubt that the type material of *Cordieria radula* Monterosato consists of the type series at MCZR.

## ACKNOWLEDGEMENTS

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# On the origin of allopatric primate species

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## ABSTRACT

Here we present a theory on the origin of allopatric primate species that follows - at least in Neotropical primates - the irreversible trend to albinotic skin and coat color, called “metachromic bleaching”. It explains why primates constitute such an exceptionally diverse, species-rich, and colorful Order in the Class Mammalia. The theory is in tune with the principle of evolutionary change in tegumentary colors called “metachromism”, a hypothesis propounded by the late Philip Hershkovitz. Metachromism holds the evolutionary change in hair, skin, and eye melanins following an orderly and irreversible sequence that ends in loss of pigment becoming albinotic, cream to silvery or white. In about all extant sociable Neotropical monkeys we identified an irreversible trend according to which metachromic varieties depart from the saturated eumelanin (agouti, black or blackish brown) archetypic form and then speciate into allopatric taxa following the trend to albinotic skin and coat color. Speciation goes either along the eumelanin pathway (from gray to silvery to cream to white), or the pheomelanin pathway (from red to orange to yellow to white), or a combination of the two. The theory represents a new and original evolutionary concept that seems to act indefinitely in a non-adaptive way in the population dynamics of male-hierarchical societies of all sociable primates that defend a common territory. We have successfully tested the theory in all 19 extant Neotropical monkey genera. Our theory suggests the trend to allopatry among metachromic varieties in a social group or population to be the principal behavioral factor that empowers metachromic processes in sociable Neotropical monkeys. It may well represent the principal mechanism behind speciation, radiation, niche separation, and phylogeography in all sociable primates that hold male-defended territories. We urge field biologists who study primate distributions, demography and phylogeography in the Old World to take our theory to the test in the equally colorful Catarrhini.

## KEY WORDS

Neotropical primates; phylogeography; metachromic bleaching; speciation; radiation.

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## INTRODUCTION

We could ask ourselves (Darwin, 1859): “*Why primates constitute by far the most diverse, species-rich and colorful Order in the Class Mammalia? Do primate diversity, metachromism and metachromic processes relate directly to sexual selection? Or, rather to its generally complex, hierarchically*

*organized social structure and male territoriality? If not sexual selection, what could be the principal factor(s) in primate social behavior to be held responsible for metachromic processes, speciation, radiation, niche separation, and phylogeography?*”

Inspired by Alfred Russel Wallace whose concept of the “Origin of Species” was laid down in a paper

he sent for review to Charles Darwin, here we introduce a new and original theory about species evolution taking place in particular in sociable territorial primates. Our theory "*On the tendency of metachromic varieties in sociable primates to depart indefinitely from the agouti archetype and evolve in advanced eumelanin, pheomelanin to albinotic bleached allopatric taxa*" is equally rooted in life-long fieldwork on socio-ecology of all Neotropical monkey genera, both in captivity and in the wild. It closely follows the principle of evolutionary change in tegumentary colors called "metachromism", a hypothesis propounded by Philip Hershkovitz (1968; 1977). Metachromism holds the evolutionary change in hair, skin, and eye melanins following an orderly and irreversible sequence that ends in loss of pigment through which a taxon of a given genus or phylogenetic clade eventually becomes albinotic, cream to white. Individual hair color or the entire coat changes from agouti (characterized by alternating blackish-brown and reddish bands on the terminal half of the hair) to uniformly blackish-brown, and thereafter to gray, and eventually to white or colorless, called the eumelanin pathway; or, it changes from agouti to uniformly reddish to orange to yellow to cream, and eventually white, called the pheomelanin pathway. The process itself is called saturation, which means the change from the primitive agouti pattern of the hair, or part of the pelage, or the entire coat, to a saturated eumelanin (blackish) or saturated pheomelanin (reddish) coloration. The dilution, or gradual reduction in the amount of pigment deposited in the growing hair, and disappearance of pigmentary colors is called bleaching (Fig. 1). In the color of the skin and iris of the eye, it follows the eumelanin pathway (brown to drab, to gray, or blue), and then it is termed depigmentation. Metachromism applies to all mammalian species. It is thought to also occur in bird feathers.

Our theory suggests that among social groups or populations of advanced intelligent, socially organized, male-territorial mammals, in particular primates, phenotypical varieties (mutants) that show slightly bleached eumelanin or pheomelanin colored skin or coat characteristics do arise indefinitely. Their melanocytes (skin cells that produce the black pigment melanin) are smaller, and for that or any other reason produce less melanin. In general, the tendency of these metachromic varieties is

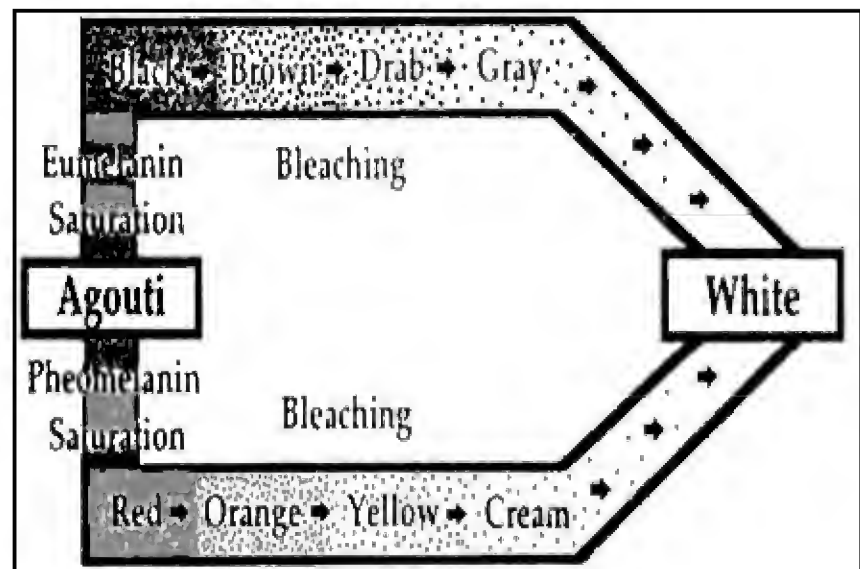


Figure 1. Bleaching from saturated eumelanin and saturated pheomelanin fields to white or colorless. Gradual reduction in the amount of pigment deposited in the growing hair results in apparent change from blackish through brown, drab gray to white or colorless in the eumelanin pathway, and from reddish through orange, yellow, cream to white in the pheomelanin pathway. Switching from the eumelanin to the pheomelanin pathway occurs in saturation but not in bleaching (modified from Hershkovitz, 1977).

neotonic, taking place locally (e.g., naked muzzle, bald head, euchromic blaze/forehead or part of the coat, depilation of skin) or all over the body. Social structure in most primate societies, in particular those of the more advanced monkeys and apes, is hierarchically organized, whereas male over female dominance is the rule, with very few exceptions (e.g., spider monkeys in the Neotropics and pygmy chimpanzees in Central Africa adopted a matriarchal social system, in which males patrol and defend a common territory, and females are allowed to transfer to neighboring social groups). Social selection is the recognition of and preference for the parental (or foster parental) phenotype in societal grouping and mating. Social selection for color or color pattern through assortative mating tends to stabilize within a chromatic range recognized and accepted by free-ranging but chromotypically imprinted members of the social group. Slightly depilated or somewhat eumelanin or pheomelanin bleached individuals deviant from the socially selected skin or hair color pattern, in particular when it is detected in adolescent to subadult males, may be discriminated against by high-ranking (alpha)-males. For that reason alone they can be pushed into the periphery of the group. Depending on the primate taxon or genus, such individual young males may also be expelled from the parental

group, and then become social 'outcasts'. Peripheral or outcast males do suffer on a daily basis from less and shorter access to the group's preferential, comparatively more nutritious food sources. They may join one another for reasons of social comfort and during ranging or foraging they tend to hang out together at the periphery of the group. Eventually, they may decide to leave the pack as all-male parties and roam around in much larger areas than just the home range or territory of the parental group. They then may attract young females from neighboring social groups. Together, they may seek some hitherto overlooked, 'empty' or little-used living space in an attempt to settle down and start their own family or social group. In case the taxon or genus it belongs to shows territorial behavior - which is the case in almost all Neotropical monkeys - these emigrants will be subsequently pushed out from neighboring territories as well. Consequently, they will die from starvation, parasite load and/or diseases forthcoming the dietary constraints they are suffering from. Or, as a matter of luck, in the end they may find some living space that is not (yet) occupied, most likely at considerable distance from the taxon's core distribution. Sometimes, such emigrant parties can be forced to survive in peripheral habitat that has to be considered marginal for that species to occur in. In extremely rare cases, such parties might even manage to circumvent a certain geographical barrier and beyond it find for the species appropriate habitat, where their specific ecological niche is not occupied, as such involving a range extension. In case that habitat is already occupied by a closely related species, a battle for life will take place and the best fitted taxon will drive the other to extinction, the red-handed tamarin *Saguinus midas* that is replacing the bare-face tamarin *S. bicolor*. Only over geological spans of time, for example after a vicariance has taken place, suitable habitat may open up where the taxon's niche is not occupied by another primate. One may imagine that along these paths small reproductively isolated founder-colonies that contain somewhat bleached and/or depilated individuals may establish themselves there. For the sake of survival alone they would unselectively interbreed or hybridize. Inbreeding then may relax stabilizing forces and stimulate or accelerate metachromic and other degenerative (= non-adaptive) processes. The more metachromic advanced each

successively isolated breeding colony is, or the farther it has moved from the center of that taxon's dispersion, the nearer it will come to the end of its metachromic evolution. And, the narrower will be its range of chromic fitness (e.g., prey and predator camouflage). This degenerative process, though, may be counterbalanced if under strong natural selection newly diverged forms, that evolve in a, for the original species marginal or new habitat, niche or landscape, at the same time selectively become better fitted, more cooperative, more inventive, or smarter in the adaptation process. This may happen every time founder-colonies successfully travel across existing geographical barriers, such as rivers, watersheds, mountain ranges, or open areas with arid scrub vegetation. Completion of the processes of metachromic bleaching, depigmentation, or depilation, whether taking place single or combined, eventually will result in extinction of the race or species. Unless the founder-colony or population in time does find and manage to occupy hitherto empty, but suitable habitat. Or: if it adapts to a different ecological niche, where skin and coat color do not have survival value by lack of competition from closely related species. Dead-end, isolated, peripheral, or new habitats may be occupied by metachromic dead-end populations, such as has happened over and over in the Neotropics in advanced albinotic callitrichids, uakaris, sakis, titis, capuchins, howlers, spider, woolly, and woolly spider monkeys.

## RESULTS

In non-territorial, peaceable Dwarf Marmosets *Callibella humilis* neotony and euchromism are clearly demonstrated as infants are overall much lighter colored than adults, showing a tendency to albinotic. Their overall pelage is light brown, their tail alternately light and dark-brown banded, and their face flesh-colored with a circumference of long, bright white hairs. From three months on, they pass through a complete metachromic metamorphosis. Their overall coat turns into saturated eumelanin, the muzzle of their faces into pinkish, and their semicrescent ocular rings or eyebrows into white (Fig. 2). This natural process may be related to slightly smaller melanocytes (skin cells that produce the black pigment melanin) producing overall less melanin.

*Callibella* stands at the base of the phylogenetic tree from which all extant Amazonian marmosets, *Cebuella* and *Mico*, have derived (Van Roosmalen & Van Roosmalen, 2003). It finds itself at the verge of extinction, for it occupies the niche of exudate gouging - that is feeding on resins ouzing out of little holes they themselves have gnawed in the bark of certain gum trees and climbers. That niche is filled in by the advanced, larger, highly territorial Amazonian marmoset genus *Mico* (its distributions are shown in figures 5–7). We believe that these aggressive, over twice as big callitrichid monkeys have displaced the non-territorial dwarf marmoset and taken over its specific feeding niche all over its former, much larger range - the entire interfluvial delineated by the Rios Madeira, Amazonas and Tapajós. The genus *Callibella* is thought to have evolved there in the late-Pliocene to early-Pleisto-

cene landscape that was dominated by lacustrine seasonally inundated clear-water igapó wetlands. Being peaceable monkeys that like their neighbor's company instead of attacking or trying to kill them apparently has not been an evolutionary success among primates (Van Roosmalen, 2013a, b; 2015).

Contrastingly, the pygmy marmoset *Cebuella* that derived from prototypic *Callibella* nowadays occupies the entire western Amazon Basin. We believe it was so successful because *Cebuella*, being allopatric with *Callibella* and *Mico*, could occupy the ecological feeding niche of exudate gouger west of the Rio Madeira. There, it did not have to face competition from other callitrichids over exudate food sources. Indeed, Amazonian tamarins (genus *Saguinus*) that range west of the Rio Madeira (Figs. 7–13) lack the elongated tusked mandibular second incisors needed for tapping sap

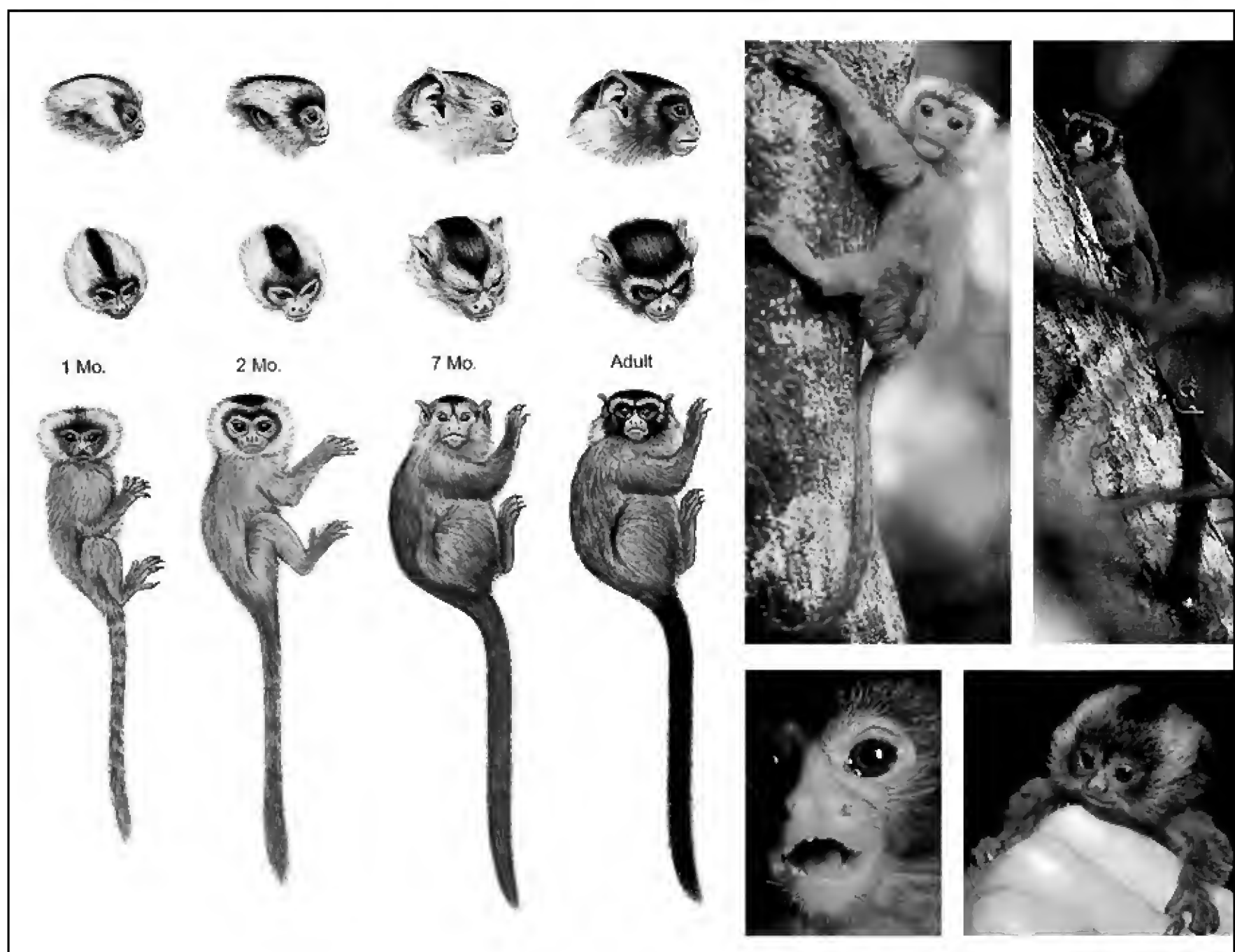


Figure 2. Ontogeny in Black-crowned Dwarf Marmosets *Callibella humilis* Van Roosmalen & Van Roosmalen (2003) based on photos of captive and wild individuals (Van Roosmalen et al., 1998).

from tree barks. As such, tamarins do not directly compete with pygmy marmosets over gum.

Instead, tamarins of different taxa are reported to parasitize on pygmy marmosets by licking the resins from tap holes made by the latter.

*Cebuella pygmaea* being overall agouti colored is clearly the most archetypic among the two extant taxa of pygmy marmoset. Distributed north of the Upper Amazon River (Rio Solimões/Río Marañón) and specialized in exudate gouging, the species (or its precursor) seems to have adapted to seasonally white-water inundated floodplain forest (várzea) habitat. Somewhat pheomelanin bleached colonizers of ancestral *C. pygmaea* (having an orange colored tail and breast, progressively bleached yellow to white belly, yellow-white mustache, naked pink-colored muzzle and circumocular rings) following the trend to allopatry once must have man-

aged to traverse the Amazon River proper, on floating várzea islands and/or passively through riverbend cut-offs (oxbow lakes). By lack of competitors the nearest to albinotic taxon *Cebuella niveiventris* - the form that derived from allopatric archetypic *C. pygmaea* - could then have extended its range from the Rios Javari and Juruá east as far as the Rio Madeira and south of the Amazon River as far as the Bolivian Amazon (Fig. 3). There, it secondarily adapted to never inundating terra firme high forest. Nowadays, it is found there, especially at edges of treefall clearings and in secondary growth. As *C. niveiventris* is fully allopatric with *C. pygmaea* and, moreover, shows completely different habitat preferences, we here propose to attribute both taxa full-species status naming them *C. pygmaea* and *C. niveiventris*. During our systematic surveys of primate distributions and diversity

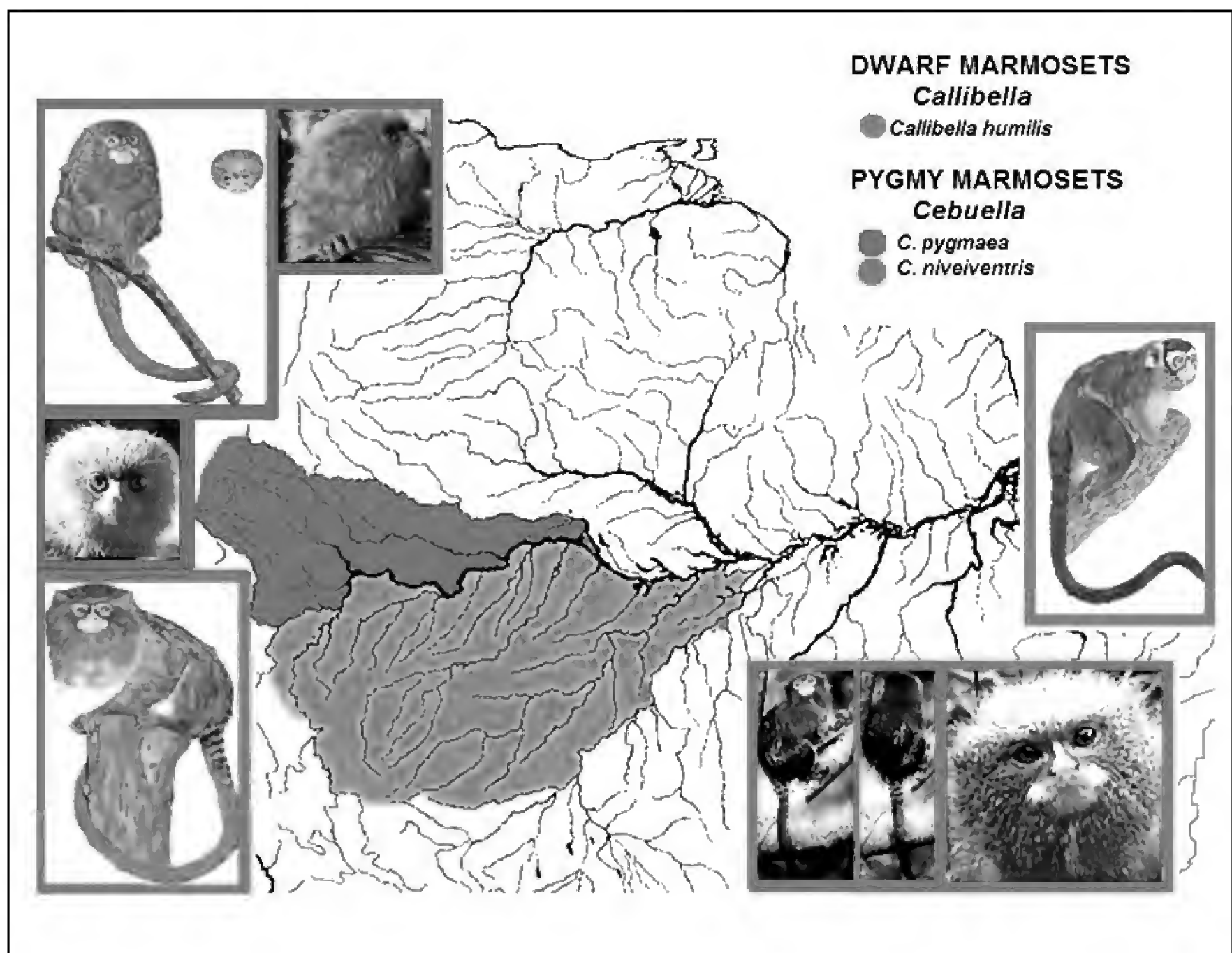


Figure 3. Present-day distributions are here depicted for Black-crowned Dwarf Marmosets genus *Callibella* and Pygmy Marmosets genus *Cebuella*, representing the smallest monkeys in the world. The current distribution of the monotypic genus *Callibella* perhaps has to be considered the smallest of any primate in the Neotropics.



carried out in the matrix terra firme hinterland stretching out behind the floodplain of white-water rivers (i.e., the Rios Javari, Juruá, Purús and Madeira), we were not able to detect any phenotypical difference between individuals sighted at any point along these far-apart rivers. It may indicate that in highly territorial monkeys like pygmy marmosets that occupy large distributions delineated by some of the largest tributaries of the Amazon River, phenotypical characters of skin and pelage coloration and/or local hair growth or depilation seem to have stabilized. In other words, we believe that within a given monkey's distribution something like a gradient of slightly differing phenotypes or color morphs, or geographic races, in reality does not exist. These and other observations from the larger field have led us to attribute full-species status to monkey taxa such as *C. pygmaea* and *C. niveiventris* that we ourselves have confirmed to be phenotypically stable throughout their (sometimes very large) range.

Here, we would like to propose a new species concept: ecospecies. This species concept is further corroborated by the here introduced evolution theory that aims to explain the origin of allopatric primate species. We define ecospecies as follows: “An ecospecies is a genetically isolated population or group of populations of a kind that does not undergo any gene flow from other populations of one or more closely related kinds, and that demonstrates a stabilized, well-defined phenotype over its entire range, in which it occupies and defends a specific ecological feeding niche against any outside competitor”. This definition of a primate species avoids the confusing, rather arbitrary distinction between species and subspecies (or race), for it adds sociobiological factors to geographical, geomorphological and phytosociological ones that act on the evolutionary process of primate speciation and radiation. Following this concept, for instance, an enclave population of *Callibella humilis* that we found living year-round in the seasonally inundated floodplain forest (igapó) along both banks of the Rio Atininga - genetically isolated from the main population occurring in terra firme forest at least one-hundred km to the north - should be given its own species name and treated as such. Or, in case the ranges of two saddle-back tamarins of the *Saguinus fuscicollis* Clade, hitherto taxonomically treated as subspecies, are separated by a con-

tact zone, where territorial behavior effectively impedes gene flow through hybridizing, both populations should be attributed full-species status.

The callitrichids Goeldi's Monkey *Callimico* and Black-crowned Dwarf Marmoset *Callibella* do represent the only monospecific (= monotypic) primate genera in the Neotropics. *Callimico* lives in the upper Amazon Basin region of Bolivia, Brazil, Peru, Colombia, and Ecuador (Fig. 4). Goeldi's monkey coat coloration is saturated eumelanin, blackish or blackish-brown. It forages in dense scrubby undergrowth of low mixed forests with discontinuous canopies and in so-called ‘tabocais’ (low forest dominated by bamboo) at levels of less than five meters. Social groups consisting of monogamous pairs with single offspring count on average six individuals. Groups live in patches of suitable habitat, often separated by miles of unsuitable vegetation. Goeldi's monkeys are vertical clingers and leapers able to leap horizontal distances of up to four meters between branches. As they are peaceable monkeys not showing any form of territoriality, Goeldi's monkeys often associate in mixed species groups with different species of tamarin *Saguinus* (Mittermeier et al., 2013). The fact that this primitive little monkey, just like the dwarf marmoset *Callibella*, remained archetypic in its blackish agouti coat coloration, is peaceable, is not showing any territorial behavior towards its neighbors, is occupying a unique feeding niche (foraging on the ground for fungi and invertebrates, and for fruits at low levels of a discontinuous canopy), and over geological time-span did not diverge into more than one taxon, strongly supports our doctrine that attributes speciation and radiation in male-territorial Neotropical primates primarily to the trend to allopatry as expressed in meta-chromic bleaching.

As shown in the schematic distribution map of all known Amazonian marmosets (Fig. 5), each interfluvium in the area delineated by the most effective riverine barriers - Rio Amazonas in the north, Rio Madeira in the west, Rio Guaporé in the south, and Rios Tapajós-Juruena and Xingú in the east - is inhabited by a different taxon of *Mico*, which species phylogeographically and phylogenetically radiated away from an ancestral, archetypic agouti-colored form much resembling the extant species *M. melanurus* (Van Roosmalen et al., 2000) from the upper Rio Aripuanã basin - the taxon with the

southernmost distribution of all Amazonian marmosets to be placed at the base of *Mico*'s phylogenetic tree.

Four monophyletic cladistic Groups or Clades are distinguished: the Bare-ear *M. argentatus* Clade, the (Tufted-ear or) Tassel-ear *M. humeralifer* Clade, the White-mantle (white-hip) *M. melanurus* Clade, and the Orange-leg *M. marcai* Clade (Figs. 6, 7). Within each Clade, the evolutionary pathway towards advanced metachromic bleached (and ultimately albinotic) taxa can be plausibly retraced. Albinotic forms in dead-end distributions may eventually go extinct (i.e., *M. chrysoleucos* in the *M. humeralifer* Clade; the new *Mico* species that occurs between the Rios Teles-Pires and Ronuro, *M. leucippe*, and *M. argentatus* in the *M. argentatus* Clade; *M. acariensis* and *M. saterei* in the *M. melanurus* Clade; and *M. manicorensis* in the *M. marcai* Clade). In territorial sociable primates the

principle of metachromic bleaching that seems to fuel the trend to allopatry is an irreversible, seemingly non-adaptive evolutionary pattern. The metachromic pathway followed within the *M. argentatus* Clade is a predominantly pheomelanin one, with first the nearest to archetypical, dark orange-colored taxon *M. emiliae* from the Rio Irirí. From *M. emiliae* diverged in southward direction the moderately bleached new species that we identified to occur between the Rios Ronuro and Teles-Pires, and northward the advanced albinotic taxa *M. leucippe* (all white with a pink face) and *M. argentatus* (all white with a black tail). The latter occupy dead-end distributions, as they are pressed at their northern limit against the untraversable Rios Tapajós and Amazonas, respectively. Within the tufted-ear or tassel-ear Clade of *Mico* the metachromic pattern followed the eumelanin pathway, from the darkest agouti-colored taxon *M. mauesi* going straight into

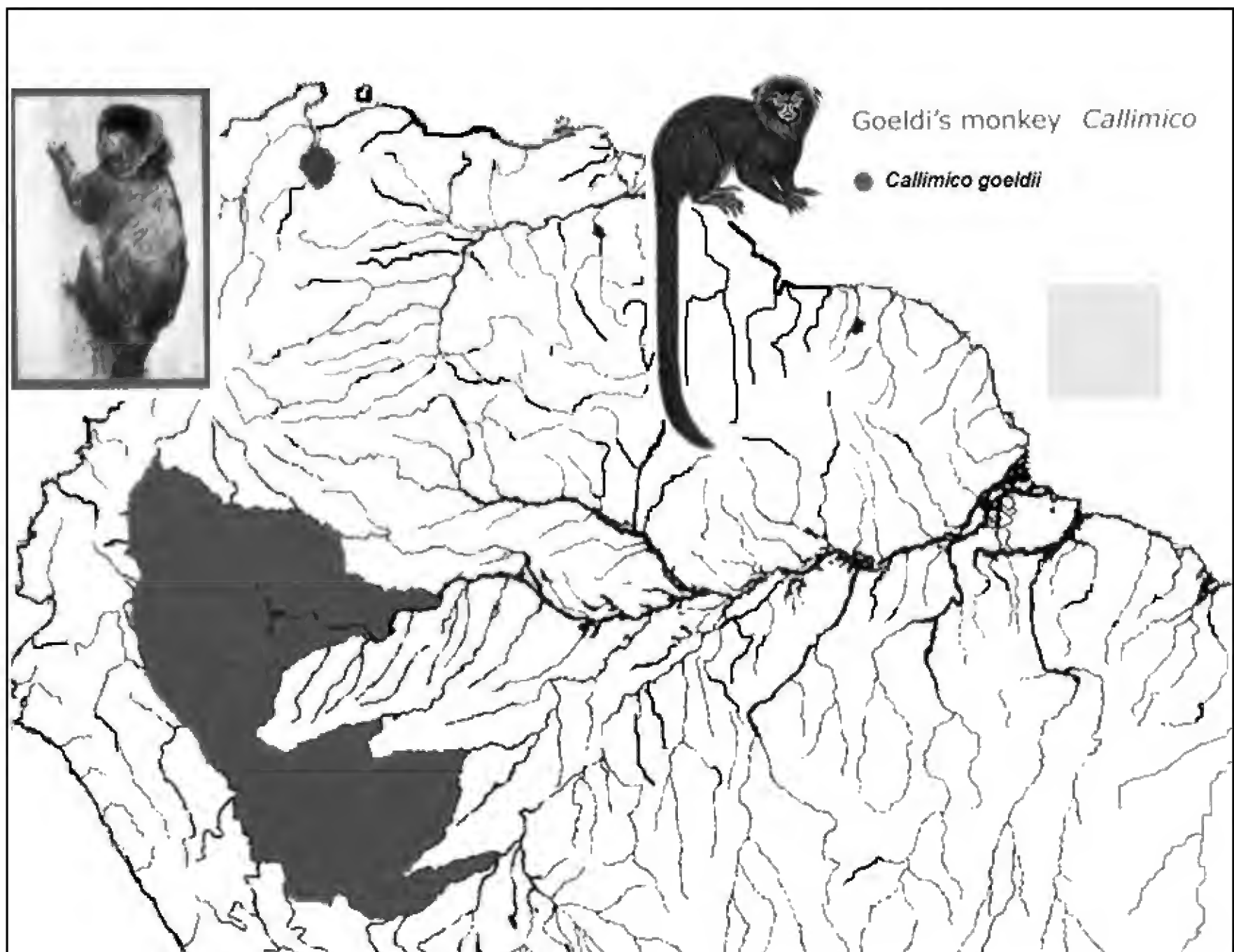


Figure 4. Present-day distribution of monotypic Goeldi's Monkey *Callimico goeldii*.

the overall whitish and gray *M. humeralifer* in the Clade's northernmost dead-end distribution (delineated by the Amazon and Tapajós Rivers). Along the pheomelanin pathway it diverged into the overall orange and white colored golden-white tassel-ear marmoset *chrysoleucos*, the species that occupies the westernmost dead-end distribution delineated by the Rios Madeira and Aripuanã. Within the white-mantle (white-hip) Clade of *Mico* the pathway followed goes from the nearest archetypic agouti-colored taxon *M. melanurus* in northern direction to the advanced pheomelanin bleached half-way albinotic taxa *M. intermedius*, *M. acariensis*, and *M. saterei*. And within the fourth Group of *Mico*, the orange-leg *M. marcai* Clade, the pathway followed in northern direction starts from the metachromic nearest to archetypic taxon *M. marcai* diverging into the advanced euchromic to almost albinotic taxon *M. manicorensis*, and in western direction proto-*marcai* evolved into the slightly but progressively bleached taxa *M. nigriceps* and *M. rondoni*, all three occupying dead-end distributions delineated by the untraversable Rio Madeira (after the Amazon River proper the second strongest river barrier in the entire Amazon Basin).

As all interfluves occupied by a different *Mico* species show dead-end distributions delineated by untraversable rivers at their northern and western limits, each species represents a different stage along the eumelanin or pheomelanin pathway that is frozen in time, but at the end of its metachromic evolution it invariably will turn into albinotic (Figs. 6, 7). Once arrived there, such primate taxa will inevitably go extinct, unless a founder-colony manages in time to cross the geographic (riverine) barrier by means of a river bend cut-off, by hopping on várzea forested floating islands, or by circumventing a geographical barrier. According to the doctrine, the evolutionary rate of metachromism is primarily controlled for by the trend to allopatry, and secondarily by environmental and genetic factors which may accelerate, retard, or terminate metachromic processes, or hold them in dynamic equilibrium, but cannot alter, reverse, or deflect them from their course. Hypothetically, growth and spread of a founder-colony of a certain Amazonian marmoset across a certain interfluve delineated by rivers, entails social selection. Effective selection stabilizes the mean chromotype of the colony at a color tone or grade inbetween that of the founders

and that of the albinotic ones towards which all monkeys tend. Amazonian marmosets (genus *Mico*) represent an advanced stock of callitrichids that evolved as late as the Pleistocene, south of the Amazon River and east of the Rio Madeira, from an ancestral stock of the *Callithrix ouistitis* occurring in Central and SE Brazil (Van Roosmalen & Van Roosmalen, 2003). About 1.5 MYA, a major vicariance took place - the break-through by the proto-Madeira River of the continental watershed running across the Chapada dos Parecis in Rondonia (Grabert, 1991). Thereafter, the entire area south of the Amazon and east of the Madeira drastically reversed its drainage pattern. Former rivers that since the beginning of the Pliocene had been draining the extensive clear-water wetlands in north-south direction, dried up. New rivers (mostly of the black-water type) arose and began to drain the area in opposite direction, from south to north. Most of these rivers emptied out in the Rio Madeira, some directly in the Amazon River. Founder-colonies at different phenotypic stages of metachromic bleaching that derived from archetypic *M. melanurus* - pushed by the trend to allopatry - subsequently invaded and inhabited the newly formed interfluvial terra firme 'islands' that new rivers had been creating. These newly available lands offered them their preferred habitat of terra firme rainforest, in which they filled the niche of exudate gouging, which niche east of the proto-Madeira River was hitherto exclusively occupied by the much smaller and peaceable, non-territorial dwarf marmoset *Callibella humilis* (Van Roosmalen & Van Roosmalen, 2003). Ever since, *Callibella humilis* seems to have lost the battle against the aggressively expanding *Mico* newcomers. Our assumption is that the dwarf marmoset has been locally driven to extinction almost all over its former range since the genus evolved in the late Pliocene. Presently, the black-crowned dwarf marmoset hangs on along the westbank of the lower Rio Aripuanã. As a commensal, it takes refuge on the terras pretas (human-made black-earth farmland) from the deadly attacks of the local Amazonian marmoset *Mico manicorensis* (Van Roosmalen et al., 2000; Van Roosmalen & Van Roosmalen, 2003). This example may well demonstrate that a specific ecological niche such as that of specialized gougers and feeders of gum (exudates) in a certain habitat (e.g., primary rain forest) can only and exclusively be occupied by a

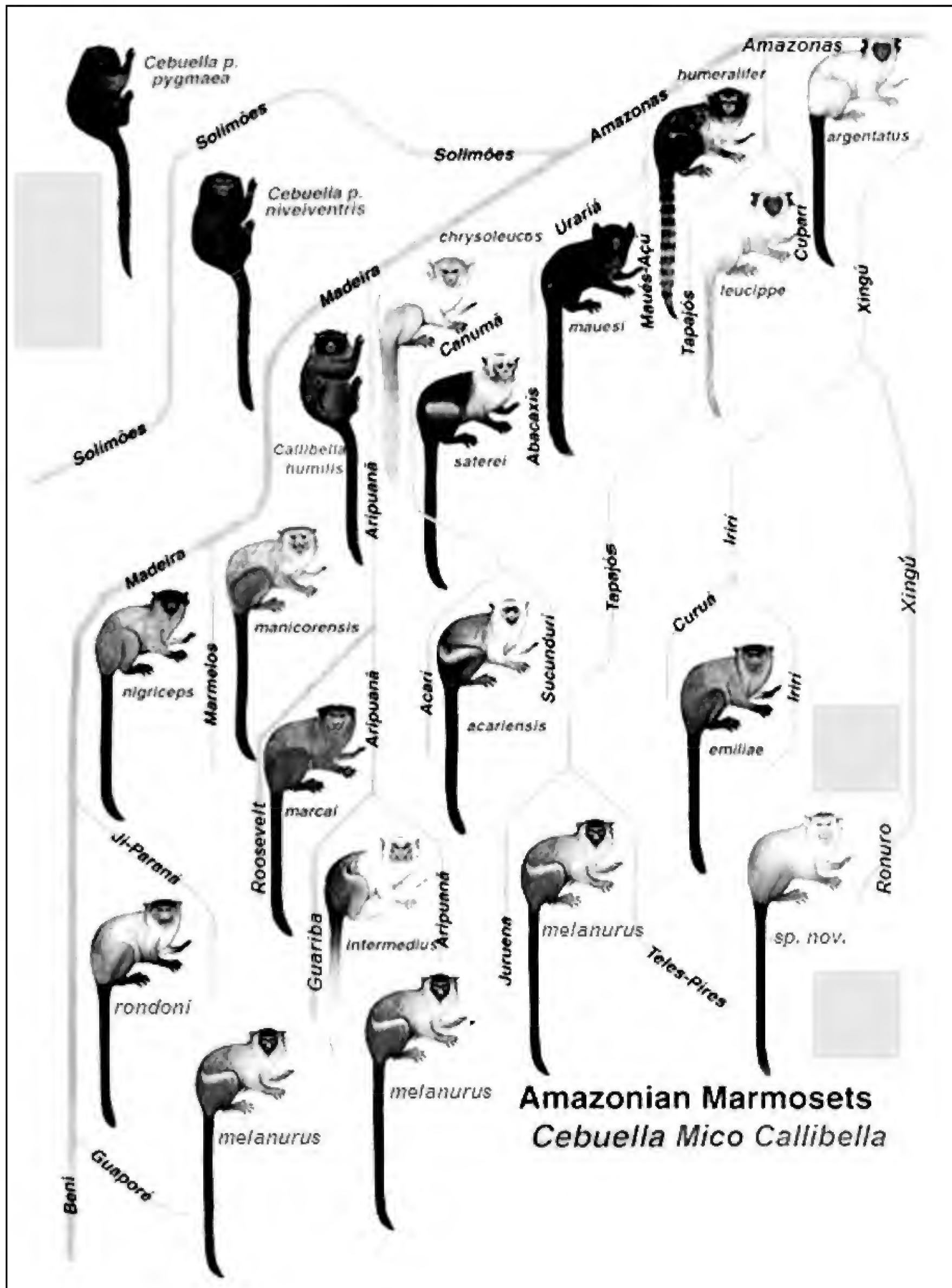


Figure 5. Schematic distributions as delineated by (for Amazonian Marmosets) untraversable rivers drawn for all known Amazonian Marmosets belonging to the genera *Callibella*, *Cebuella*, and *Mico*.



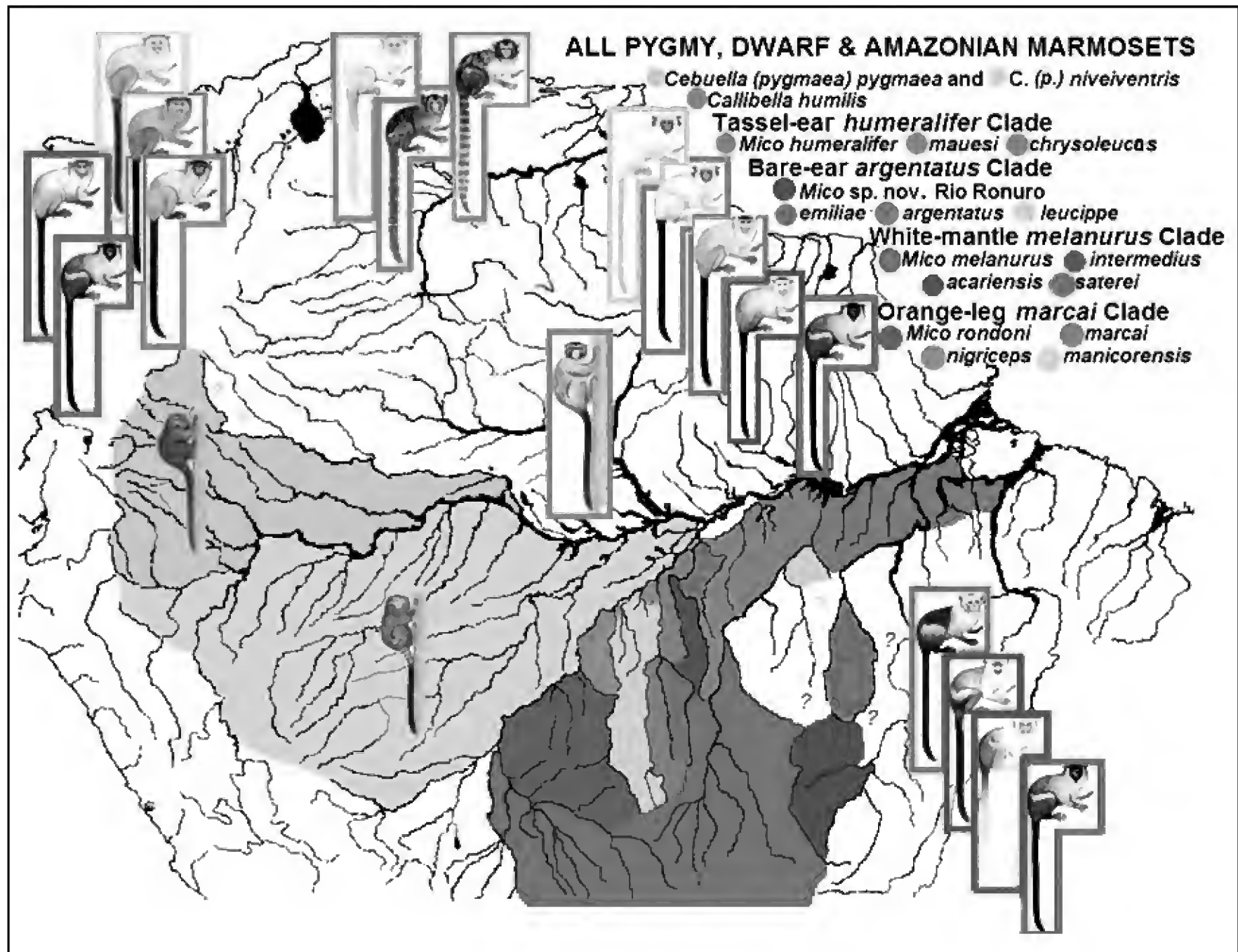


Figure 6. Geographical distributions delineated by rivers drawn in one map for all known Amazonian Marmosets that belong to the marmoset genera *Callibella*, *Cebuella*, and *Mico*.

single taxon that defends it, in this case even beyond generic bounds.

Figures 5–7 demonstrate that about all interfluvies occupied by a single species of *Mico* show dead-end distributions delineated by for rainforest habitat-specialists untraversable rivers at their northern and western limits. At their southern limits, all distributions invariably show a mostly narrow open-end, where a contact zone between two adjacent distributions must exist. Hybridization between Amazonian marmosets, though, has never been seen or reported in the wild. This may well be attributed to strong social and sexual selection. Indeed, all Amazonian marmosets of the genus *Mico* developed hypertrophied external genitalia in each gender that are physically greatly differing among related taxa (Van Roosmalen et al., 2000) (Figs. 8–11).

We ourselves have kept, raised and bred with a number of Amazonian marmosets, both in free-ranging and captive conditions. Expressive and often violent territorial behavior of all members of a social group, aside of species-specific sexual display of external genitalia, pheromones and scent-marking of one another's coat, has always prevented our marmosets from hybridizing (interspecific cross-breeding). For instance, we kept breeding social groups of all three taxa of the tassel-ear *M. humeralifer* Clade (i.e., *M. humeralifer*, *M. mauesi*, and *M. chrysoleucos*). To avoid one group from wiping out the other, we had to keep different species in separate cages, whereas we let only one group of *M. chrysoleucos* free-ranging in the forest that surrounded the compound. Even so, adults were still seen trying to grab and bite one another through the fine-mesh wire. From our unique exper-



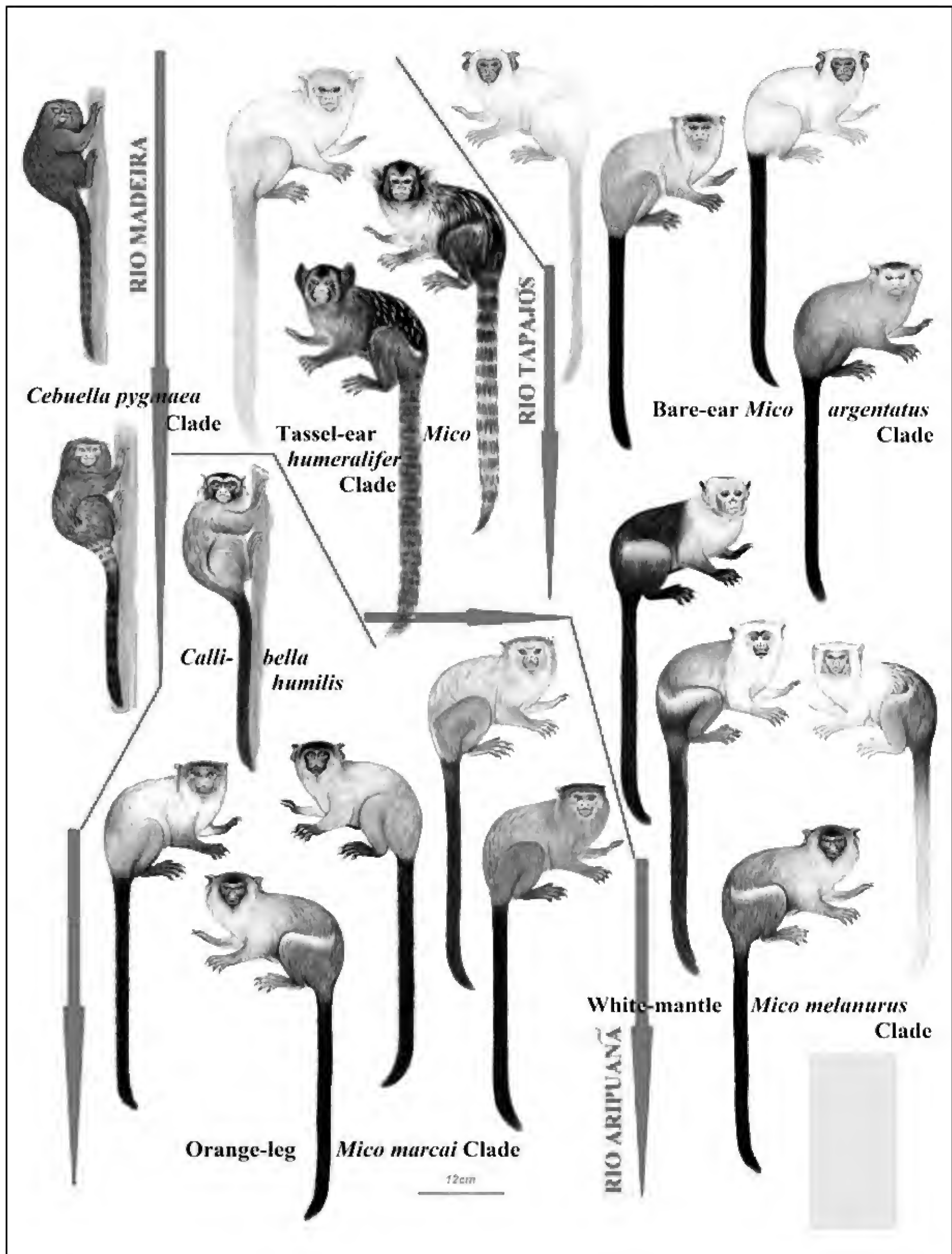
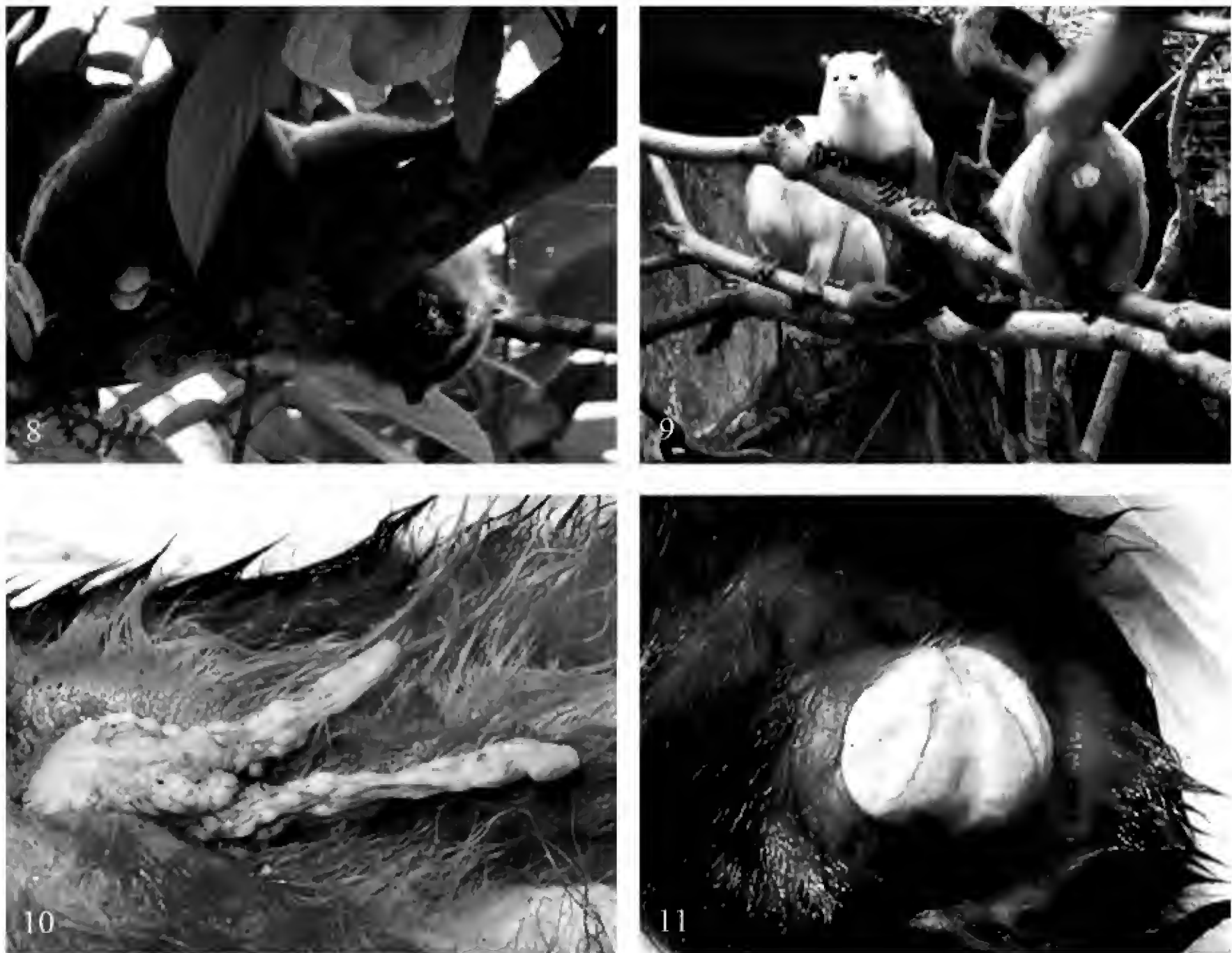


Figure 7. Radiation and metachromic diversification following eumelanin and pheomelanin pathways of metachromic bleaching depicted for all recognized phylogenetic Clades of Amazonian (*Mico*), Dwarf (*Callibella*), and Pygmy Marmosets (*Cebuella*) depicted to scale.



Figures 8–11. In all taxa of *Mico*, both males and females evolved hypertrophied, species-specific, in anatomical respect very differently shaped external genitalia. Fig. 8: male *M. manicorensis* sexually displaying; Fig. 9: exposed pudenda in adult female *M. acariensis*; Fig. 10: pudenda with 2 cm long vaginal lips in *M. saterei*; Fig. 11: pudenda in *M. acariensis*. This feature supports our view that all taxa of *Mico* should be considered different species and not just metachromic color morphs.

ience having kept all kinds of marmosets (until today, not a single zoo in the world has any *Mico* on exhibit) and other callitrichids, both in captivity and free-ranging in a tropical rainforest environment, we believe that where adjacent distributions of two species of *Mico* are not defined by an untraversable river, a sharp-lined contact zone must exist, where cross-breeding never takes place. This assumption concurs with the principle of metachromic bleaching being irreversible. In theory, only through cross-breeding with a darker, overall more saturated eumelanin taxon the metachromic pathway to albinotic could be reversed, something, however, that will never happen in the wild.

As all *Mico* do display strong interspecific territorial behavior - each group defending its living space by means of (often ritualized) territorial

boundary conflicts - within a given contact zone cross-breeding will not take place between neighboring groups of different but related ecospecies, as distance is maintained by regularly performed boundary conflicts. This way, any gene flow between phenotypically different populations is impeded. In phylogeographic terms, the farther radiated away from the origin of a Clade's dispersion - that of the nearest to archetypic species within a monophyletic Clade - the more progressively bleached the species will become. Partly or fully albinotic taxa, therefore, often occur in or near the Clade's dead-end distributions.

In figures 12–15, we have visualized the phylogeographic distributions, radiation, and supposed pathways of metachromic bleaching of all known Tamarin Monkeys genus *Saguinus*. We have di-

vided them up in the following monophyletic Groups or Clades: the Saddle-back Tamarins of the *S. fuscicollis* Clade (Fig. 13); the Black-mantle White-mouth Tamarins of the *S. nigricollis* Clade in one map combined with the Mustached Tamarins of the *S. mystax* Clade, the Red-chested Mustached *S. labiatus* Clade, and the Emperor Mustached *S. imperator* Clade (Fig. 14); and the Bare-face Tamarins of the *S. midas*, *S. bicolor* and *S. geoffroyi* Clades (Fig. 15). To complete the callitrichid picture, we have visualized the distributions of the Lion Tamarins genus *Leontopithecus*, and the True Marmosets or Ouistitis genus *Callithrix*, from SE Brazil (Fig. 16).

In geological history, speciation and radiation within the Saddle-back Tamarins of the *S. fuscicollis* Clade (Figure 13) went along two pheomelanin pathways of metachromic bleaching: one sub-Clade radiated south of the Amazon River from east to

west, from the most saturated eumelanin, nearest to archetypic taxon *S. mura* (green distribution) to the completely albinotic all-white taxon *S. melanoleucus* (blue distribution) via the taxa *S. avilapiresi*, *S. fuscicollis*, and *S. cruzlimai*. The bleaching process took first place in the head parts - muzzle and blaze - and, after having traversed the Rio Juruá back to its right bank, the metachromic bleaching process completed from the overall orange-colored taxon *S. cruzlimai* into the fully albinotic taxon *S. melanoleucus*. Another radiation took place from *S. mura* directly into *S. weddelli*, and, after having traversed the Rio Purús, into the overall light-brown colored taxon *S. primitivus* - both with a fully albinotic blaze and muzzle/mouth. A second sub-Clade of saddle-back tamarins radiated from the Peruvian Amazon in eastern direction, from the saturated eumelanin nearest to archetypic taxon *S. leucogenys* (light blue distribution) into the slightly

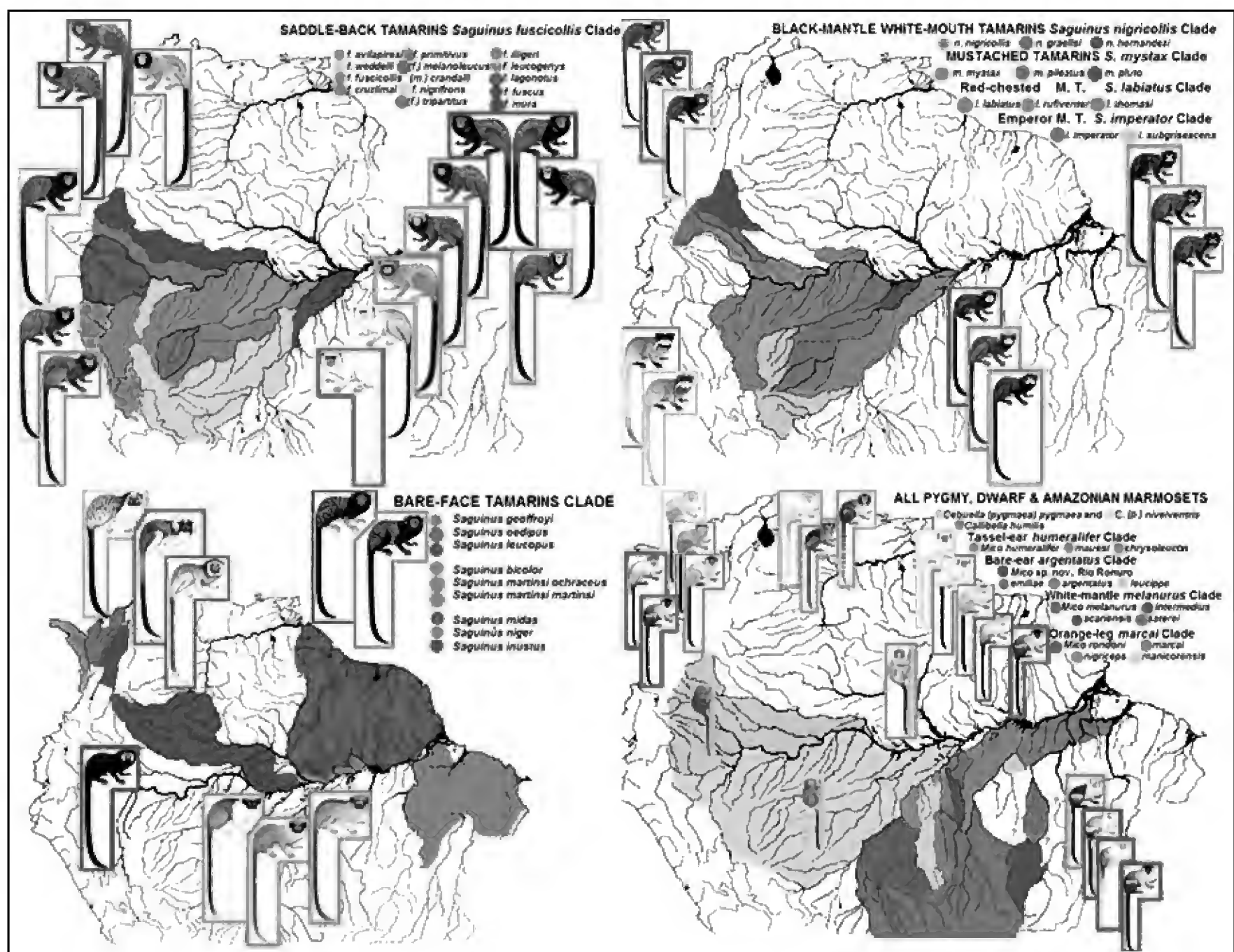


Figure 12. Distributions of all Neotropical Tamarin Monkeys, genus *Saguinus*, compared with those of all Amazonian Marmosets.

bleached taxa *S. illigeri* and *S. nigrifrons*, and after crossing the upper Amazon River (where it is called Río Marañón) northward into the progressively bleached taxa *S. lagonotus*, *S. fuscus*, and *S. tripartitus*, the latter three taxa being distributed north of the Amazon River in the Ecuadorian, Colombian, and Brazilian Amazon.

Within the Black-mantle White-mouth Tamarins of the *S. nigricollis* Clade (Fig. 14) that is distributed only north of the Amazon River in the Brazilian, Ecuadorian and Colombian Amazon, the nearest to archetypic saturated eumelanin taxon is *S. nigricollis*. It radiated northwestward and diverged into the slightly bleached taxa *S. graellsii* and *S. hernandezi*. The *S. nigricollis* Clade is sympatric with the saddle-back tamarins of the taxa *S. lagonotus*, *S. tripartitus* and *S. fuscus* (Fig. 13). However, they occupy different ecological niches and therefore can be seen traveling and foraging in mixed species associations, with the larger-sized black-mantle tamarins in the lead and staying higher up in the canopy of the terra firme rain forest. Within the Emperor Mustached Tamarins of the *S. imperator* Clade both extant taxa are already progressively bleached, the grayish taxon *S. subgriscescens* slightly more so than *S. imperator*. In the upper Rio Purús region there must exist a narrow contact zone between the two taxa along the southernmost open-end distribution of *S. imperator*. Within the Red-chested Mustached Tamarins of the *S. labiatus* Clade, *Saguinus labiatus* occupies the southernmost distribution and represents the nearest to archetypic taxon with a dark red chest and thin-lined white mustache. It radiated north of the Rio Ipixuna and diverged into the advanced orange-chested taxon *S. rufiventer* that has a more bleached white mustache and head-stripe. The third taxon of the *S. labiatus* Clade is *S. thomasi* the precursor of which once must have traversed the Rio Solimões. It might have been replaced later by *S. inustus* north of the Rio Solimões as far west as the Rio Japurá. *Saguinus thomasi* nowadays only occupies the lower Rios Solimões/Japurá interfluvium. It represents the most progressively pheomelanin bleached taxon of the *S. labiatus* Clade in its light orange-colored chest and the broad-lined triangular white mustache. Within the mustached tamarins of the *S. mystax* Clade, the more saturated eumelanin, nearest to archetypic form is represented by the taxon *S. mystax* that is distributed west of the Rio

Juruá. After traversing the Rio Juruá, the Clade has radiated eastward while further bleaching along the pheomelanin pathway into the orange-crowned taxon *S. pileatus*, and along the eumelanin pathway diverging directly from *S. mystax* into *S. pluto*. The latter taxon is overall more grayish and has a distinctive albinotic spot around the base of the tail. In the lower Rios Juruá/Purús interfluvium we have sighted *S. pluto* ranging always in mixed-species association with the smaller saddle-back tamarin *S. avilapirezi*, with *S. pluto* always in the lead and *S. avilapirezi* rushing behind and below the group of *S. pluto* in the lower strata of high forest, always in a hurry feeding on *S. pluto*'s left-over food items.

A hypothetical pathway of allopatric speciation, radiation and metachromic bleaching followed by the Bare-face Tamarins of the *S. midas*, *S. bicolor* and *S. geoffroyi* sub-Clades may have had its origin in the Guianas (Fig. 15). An all-black, saturated eumelanin archetypic precursor of *S. midas* may once have traversed the lower Rio Amazonas and speciated allopatrically into the black-handed taxon *S. niger*. Or vice-versa (archetypic black-handed *S. niger* may once have traversed the lower Rio Amazonas and speciated allopatrically into the red-handed *S. midas*). The same or another all-black precursor of *S. midas* may have traversed the Rio Negro and allopatrically speciated into the taxon *S. inustus* that is all-black with a white-mottled face. *Saguinus inustus* nowadays occupies the entire interfluvium between the Rio Negro in the north, and the Rios Solimões, Japurá and Caquetá in the south. A founder-colony of a predecessor of *S. inustus* driven by the trend to allopatry may then have ventured from the taxon's westernmost distribution into the NW Colombian Río Magdalena basin. Once having inhabited the Río Magdalena basin, it may have diverged along a pheomelanin pathway into the extant taxon *S. leucopus* that has a white-hairy facial circumference similar to *S. inustus*. *Saguinus leucopus* then may have radiated further into the progressively pheomelanin bleached, almost euchromic taxon *S. oedipus*, and from there into the near-albinotic taxon *S. geoffroyi* that is distributed from extreme NW Colombia into Panama, as such the farthest away from the center of dispersion of the Bare-face Tamarin Clade. With respect to the three derived euchromic taxa of the *S. bicolor* Clade, as we have mentioned elsewhere, these taxa find themselves in the process of being



rigorously displaced from their respective territories by the now sympatric archetypic saturated eumelanin red-handed tamarin *S. midas*. All three taxa (i.e., *S. bicolor*, *S. martinsi*, and *S. ochraceus*) find themselves pushed with the back against the untraversable Rio Negro and/or Rio Amazonas (Fig. 15). At present, the red-handed tamarin *S. midas* is wrapping up the last stage of its range extension towards the south to the cost of all three Bare-face Tamarins of the *S. bicolor* subClade. This battle over a specific ecological (feeding) niche, in which two sympatric, closely related primate taxa are involved, will inevitably lead to the extinction of the most euchromic among the two, that is the Bare-face Tamarins of the *S. bicolor* sub-Clade: the taxa *S. bicolor*, *S. martinsi*, and *S. ochraceus* (Fig. 15).

The eumelanin *S. midas* sub-Clade might have originated in the Guianas north of the watershed with the northeastern Amazon formed by the Tumac-Humac Mountains and the open wet savannas of Roraima and Pará. A predecessor of the *S. midas* sub-Clade, perhaps the extant *S. midas* itself, once may have circumvented the watershed between the Guianas and Brazil by traversing the Parú Savanna, whereafter it may have penetrated far southwards into the northeastern quadrant of the Brazilian Amazon. We assume that before some vicariance took place this vast territory or a large part of it was inhabited by precursors of the closely related Bare-face Tamarins of the *S. bicolor* sub-Clade. Apparently, as the two sub-Clades do occupy the same ecological niche, (proto)-*midas* subsequently has displaced (proto)-*bicolor* over most of its former range. This battle is still being fought over between *S. midas* and each taxon of the *S. bicolor* sub-Clade, but it seems to come close to its end. The process of replacement is accelerated by deforestation and other human disturbance such as road-building that has taken place north of the rapidly expanding megacity of Manaus. This ongoing story clearly demonstrates interspecific intolerance in closely related territorial monkeys that occupy and exploit the same ecological niche. It inevitably leads to displacement, or sooner or later extermination of the more progressively bleached (euchromic) taxon. This kind of replacements may take place after a geographic barrier has been successfully overtaken by the more saturated eumelanin (more adaptive and/or aggressive?) of two related

taxa. Or: after a vicariance has removed a hitherto gene-flow impeding geographic barrier inbetween the distributions of two or more closely related species.

Vicariance (from Latin *vicarius*) means a process by which the geographic range of an individual taxon, or an entire biota, is split into discontinuous parts by the formation of a physical barrier to gene flow or dispersion.

Today, the *S. bicolor* sub-Clade only inhabits a 20–30 km narrow strip of terra firme rain forest alongside the southernmost edge of the Pre-Cambrian Guayanan Shield.

The three bicolor taxa are so to speak pushed with the back against rivers that happen to be the widest and most difficult to traverse on the entire South-American continent: the Rios Negro and Amazonas. The three extant taxa of Bare-face Tamarins each occupy what is called a “dead-end distribution”. The distribution of the half-brown, half-white taxon *S. bicolor* measures not more than 20–30 x 200 km, delineated in the west and south by the Rios Cuieiras, Negro, Amazonas, and Urubú. Bicolor’s neighbor to the east - the almost fully bleached, ochraceous colored taxon *S. ochraceus* - occupies the interfluvium between the Rios Urubú and Uatumã. To the east of its distribution, the pheomelanin, light orange-colored taxon *S. martinsi* occupies the lower interfluvium between the Rios Uatumã and Nhamundá (Fig. 15). Disputedly, a now extinct precursor of the Bare-face *S. bicolor* sub-Clade that once ranged somewhere to the north of the Amazon River, may have driven the three extant taxa of the *S. bicolor* subClade - each at a different stage of metachromic bleaching - into the small interfluvial dead-end distributions, that they occupy today. The saturated eumelanin (blackish-brown) red-handed tamarin *S. midas* that later expanded its range to the south, is now simultaneously invading the three remaining adjacent interfluvial stronghold territories of the *S. bicolor* sub-Clade.

A sharp-line contact zone drawn between *S. midas* and *S. bicolor* territory has been notified by us in the early 1990s to run at 28–30 km north of and parallel to the Negro and Amazon Rivers. While running a halfway house for orphaned monkeys situated right at the edge of the contact zone, we have repeatedly witnessed different social groups of *S. midas* raiding resident family groups of *S. bicolor*. These incidents invariably ended up



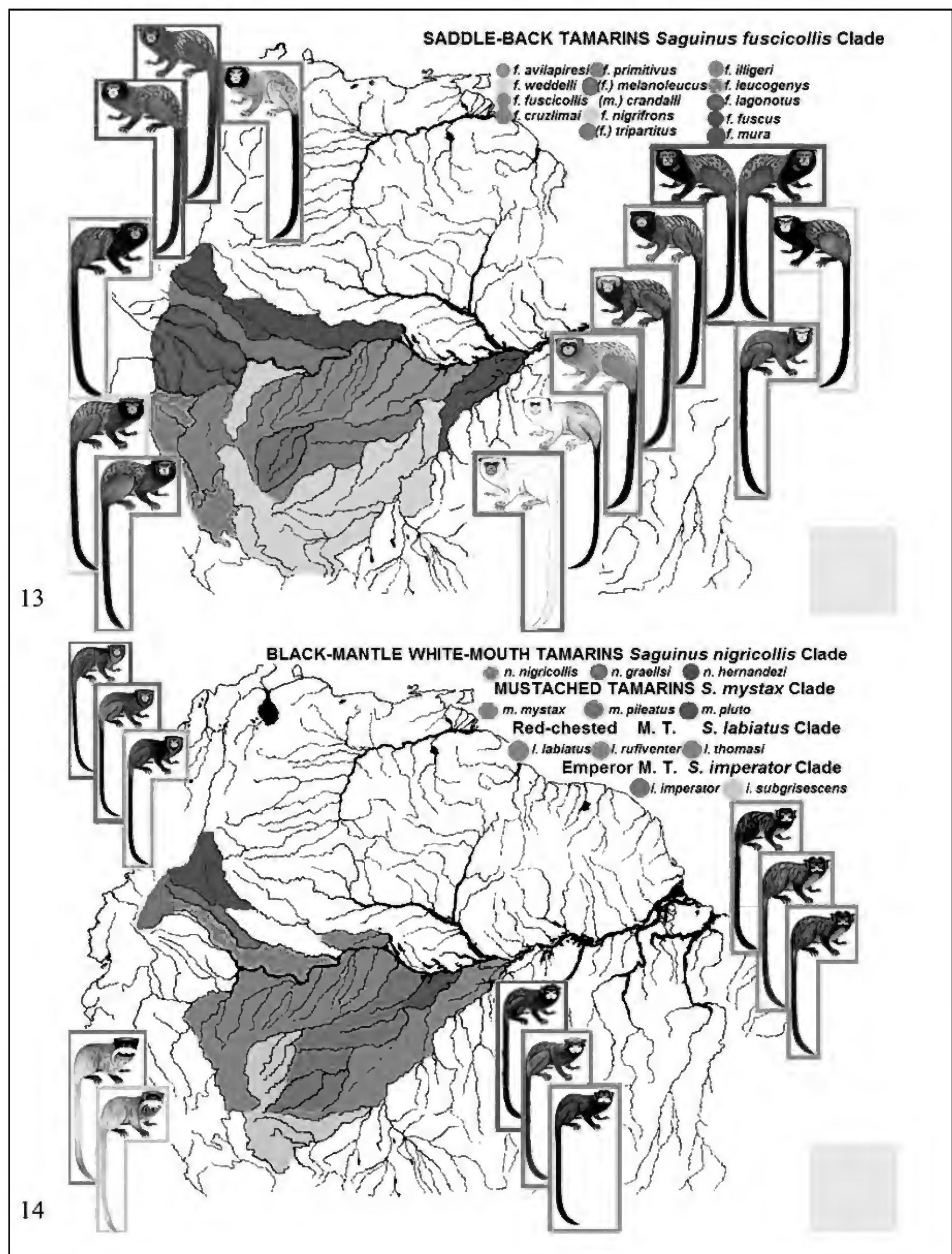


Figure 13. Distributions, allopatric speciation, radiation, and supposed pathways of metachromic bleaching in all known Saddle-back Tamarins of the *Saguinus fuscicollis* Clade. Figure 14. Idem, in the more robust, larger-sized Black-mantle White-mouth Tamarins of the *S. nigricollis* Clade, the Emperor Mustached Tamarins of the *S. imperator* Clade, the Red-chested Mustached Tamarins of the *S. labiatus* Clade, and the Mustached Tamarins of the *S. mystax* Clade.

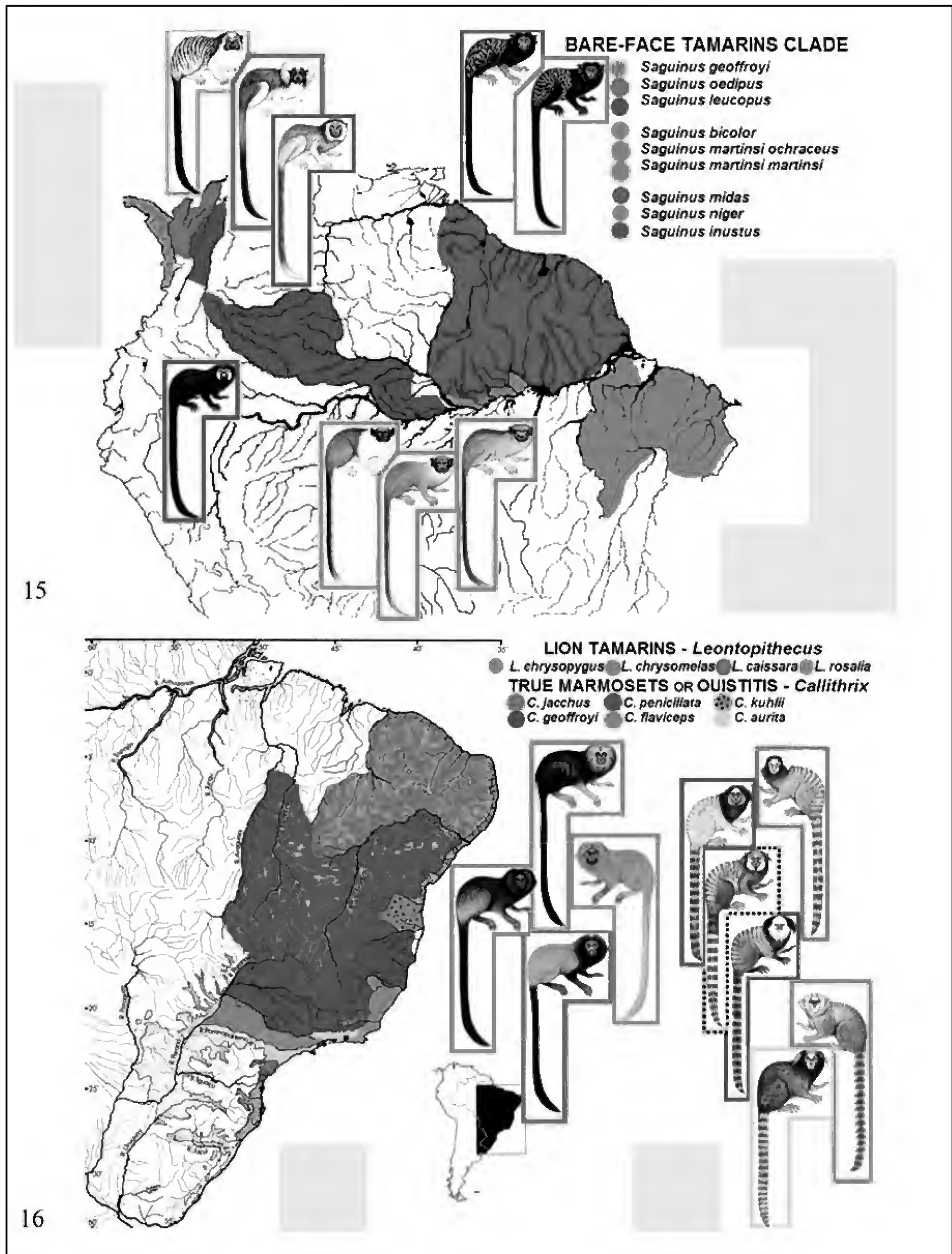


Figure 15. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all extant Bare-face Tamarins that belong to the *Saguinus midas*, *S. bicolor*, and *S. geoffroyi* sub-Clades. Figure 16. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known True (or Atlantic Forest) Marmosets (genus *Callithrix*) and Lion Tamarins (genus *Leontopithecus*) from SE Brazil.

in the defensive, less aggressive (more sensitive?) *S. bicolor* bitten to death. Now, about twenty years later, *S. midas* has extended its range at least five km further to the south to the cost of *S. bicolor* occupied territory. As *S. midas* is more opportunistic and flexible in its habitat preferences - venturing also into secondary growth and edge habitats such as roadsides - it rapidly penetrates into *S. bicolor* territory, at some places (e.g., Ducke Reserve) already reaching the outskirts of Manaus. Running a rehabilitation center for orphaned monkeys, we sometimes received whole families of *S. bicolor* that were rescued from isolated pockets of forest in urbanized areas. After some time spent in quarantine, we used to put them in large cages built on poles in the middle of the rain forest about thirty km north of Manaus in an attempt to reintroduce the species where we assumed it had occurred not long before. One day before releasing a wild-caught social group of 8 *S. bicolor*, we found them all bitten to death inside the cage that was fenced with galvanized small-meshed wire. The only animal left alive in the cage was a wild adult *S. midas* that apparently had not found back the little hole in the wire through which he and some other family members had entered the cage that very morning. On the other hand, a hand-tame *S. midas* infant that we raised free around the compound at the time, one day was 'kidnapped' and adopted by the wild *S. midas* group that roamed around in the project area.

Within the True (Atlantic Forest) Marmosets or Ouistitis genus *Callithrix* we distinguish two monophyletic Clades: the *Ca. penicillata* Clade and the *Ca. aurita* Clade (Fig. 16). Within the first monophyletic Clade we consider *Ca. penicillata* the nearest to archetypic, most saturated eumelanin taxon that occupies the largest distribution (dark green area). From there, it radiated in northern direction and diverged into the overall progressively bleached taxon *Ca. jacchus* that has fully albinotic ear-tufts. In eastern direction, from it derived and radiated away the taxa *Ca. kuhlii* and *Ca. geoffroyi* that are progressively bleached euchromic to albinotic in their mantle and head parts (except the black ear-tufts). Their dead-end distributions are pressed against the Atlantic coast. Interestingly, *Ca. kuhlii*'s range fully overlaps with that of *Leontopithecus chrysomelas*. The *Ca. aurita* Clade has *Ca. aurita* representing the nearest to archetypic, overall metachromic agouti taxon that ranges allopatric

with the lion tamarins (*Leontopithecus*) in the Atlantic forest of SE Brazil. From there derived the near albinotic taxon *Ca. flaviceps* that occupies a small area in SE Minas Gerais, allopatric with *Ca. geoffroyi* (Mittermeier et al., 2013).

As for the Lion Tamarin genus *Leontopithecus*, we consider the overall saturated eumelanin, almost all-black taxon *L. chrysopygus* the nearest to archetypic lion tamarin. From it derived in southeastern direction the taxon *L. caissara* that followed a metachromic pathway of pheomelanin bleaching in its bright orange-colored dorsal parts while maintaining the saturated eumelanin black tail, arms, legs, mantle and head of *L. chrysopygus*. Its small range in coastal Paraná State represents the southernmost distribution of any callitrichid. From *L. chrysopygus* derived in northeastern direction along a pathway of pheomelanin bleaching the two other taxa, *L. chrysomelas* and *L. rosalia*. *Leontopithecus chrysomelas* bleached in the orange colored lower arms and legs, and in the light orange to cream-white head and mantle maintaining the rest of its body saturated eumelanin. *Leontopithecus rosalia*, in turn, is evenly light orange-colored over its whole body, with the tail becoming almost albinotic. Both taxa occupy small dead-end distributions in the Atlantic forest along the coast of SE Brazil (Mittermeier et al., 2013).

In a further attempt to falsify the principle of metachromic bleaching and the crucial role we believe it plays in allopatric speciation of (at least) Neotropical monkeys, we now will proceed to examine currently known distributions, allopatric speciation and radiation, and the pathways of metachromic bleaching supposedly followed in all other male-territorial Neotropical monkey genera (i.e., *Callicebus*, *Saimiri*, *Cacajao*, *Chiropotes*, *Pithecia*, *Lagothrix*, *Ateles*, *Brachyteles*, *Alouatta*, *Cebus*, *Sapajus*, and *Aotus*).

Titi Monkeys of the genus *Callicebus* are strongly territorial in behavior, a family marking its territory vocally - a pair calling in duet, or a whole family calling in chorus. In the Amazon, a single taxon of the Collared Titi *Cal. torquatus* Group may occur in sympatry with a single titi of any of the other Non-collared Titi cladistic Groups, once the former titis are only found high up in the canopy of primary terra firme rain forest. Collared titis occupy a different, more frugivorous feeding niche than the titis that lack the white collar. The latter prefer the

lower strata and edges of terra firme rain forest, secondary growth, and savanna forest, being overall more omnivorous in their diet that contains also young leaves and insects, in addition to pulpy fruits (Hershkovitz, 1988; Hershkovitz, 1990; Mittermeier et al., 2013).

In figures 17–20, we show the distributions of all known Titi Monkeys genus *Callicebus*. Within the titi monkeys five phylogenetic cladistic Groups or Clades are recognized: *Cal. personatus* (southeastern Brazilian taxa), *Cal. torquatus* (Amazonian collared taxa), *Cal. moloch*, *Cal. cupreus* and *Cal. donacophilus* (Amazonian non-collared taxa) (Van Roosmalen et al., 2002). Within each titi Clade the irreversible pathway of metachromic bleaching towards partly or fully albinotic, from saturated eumelanin and saturated pheomelanin fields to white or colorless, is clearly demonstrated. The farther radiated away from the prototypic agouti or saturated eumelanin (black or dark brown) taxon - *Cal. melanochir* in the *Cal. personatus* Group, *Cal. medemi* in the *Cal. torquatus* Group, *Cal. cinerascens* in the *Cal. moloch* Group, *Cal. brunneus* in the *Cal. cupreus* Group, and *Cal. modestus* in the *Cal. donacophilus* Group - the more its pelage turns into orange, yellowish or cream to white, first in certain parts of the body, and eventually all over its coat. Near-albinotic forms in dead-end distributions (e.g., *Cal. pallescens*, Rio Xingú titi, Rio Mamurú titi) are doomed to eventually go extinct, as metachromism with the trend to allopatry as the driving behavioral factor is an irreversible, initially seemingly non - adaptive evolutionary pattern in all territorial monkeys. As shown in the maps, in the Amazon all distributions of titis without a white collar are occupied by just a single taxon and are delineated by rivers that function as (for titis that cannot swim) strong geographic barriers. Narrow contact zones between adjacent interfluvial distributions surely do exist, usually near the headwaters, but nowhere interbreeding or hybridization between the two neighboring taxa has been reported to take place.

Our extensive primate surveys carried out throughout the entire Amazon Basin have revealed that, in general, a given monkey taxon looks phenotypically identical throughout its entire range. In contact zones or across opposite banks of rivers that demographically separate two phylogenetically related taxa, we have noticed interspecific boundary conflicts and vocal battles to occur regularly, in

particular performed by social groupings of titis, howling monkeys and spider monkeys. In at least one contact zone between two differently looking titis we have been able to perceive the ‘trend to allopatry’ put in motion in metachromic bleached individuals that were deviant from the commonly seen phenotype. At the far northeastern corner of the distribution of Hoffmann’s Titi Monkey *Cal. hoffmannsi* a small founder-population of an albinotic all-creamwhite form, that we provisionally named the “Rio Mamurú titi”, apparently has been pushed into a dead-end distribution between the right bank of the lower Rio Mamurú, the for titis inhospitable várzeas (seasonally white-water inundated floodplain forest) along the right bank of the Rio Amazonas, and the parapatric distribution of *Cal. hoffmannsi* to the east and south as far as the lower Rio Tapajós (Fig. 17). Only mtDNA sequences may determine what taxonomic status we should allocate to this new, fully euchromic taxon: ‘color morph’ or ‘taxon in the making’. A color morph of *Cal. hoffmannsi*, a subspecies to be named *Cal. hoffmannsi mamuruensis*, or a valid new species to be described as *Cal. mamuruensis*? As mentioned before, here our ecospecies concept could be applied in case the population has been confirmed to be allopatric and genetically isolated (not allowing any gene flow) from the taxon it derived from, or when the enclave population has successfully adapted to a different ecological niche - in this case turning itself into a várzea versus terra firme rainforest habitat specialist. Our ecospecies concept (hereafter named ESC) in combination with the phylogenetic species concept (PSC) is, at least in the field, more practical, less arbitrary, and better defined, in particular when used for the purpose of species and biodiversity conservation. The ESC would put an end to the academic discussion about the arbitrary and controversial subspecies/race concept.

As Groves (2001a; 2001b; 2004; 2005) points out: “*There is no official taxonomy*”. The numerous concepts as to what is and what is not a species are controversial, and every named species is itself nothing more than a hypothesis. Our understanding of the systematics of the primates is constantly growing, not only through the discovery of new species but also with new information brought to bear from diverse fields such as morphology, cytogenetics, molecular genetics, paleontology, biogeo-



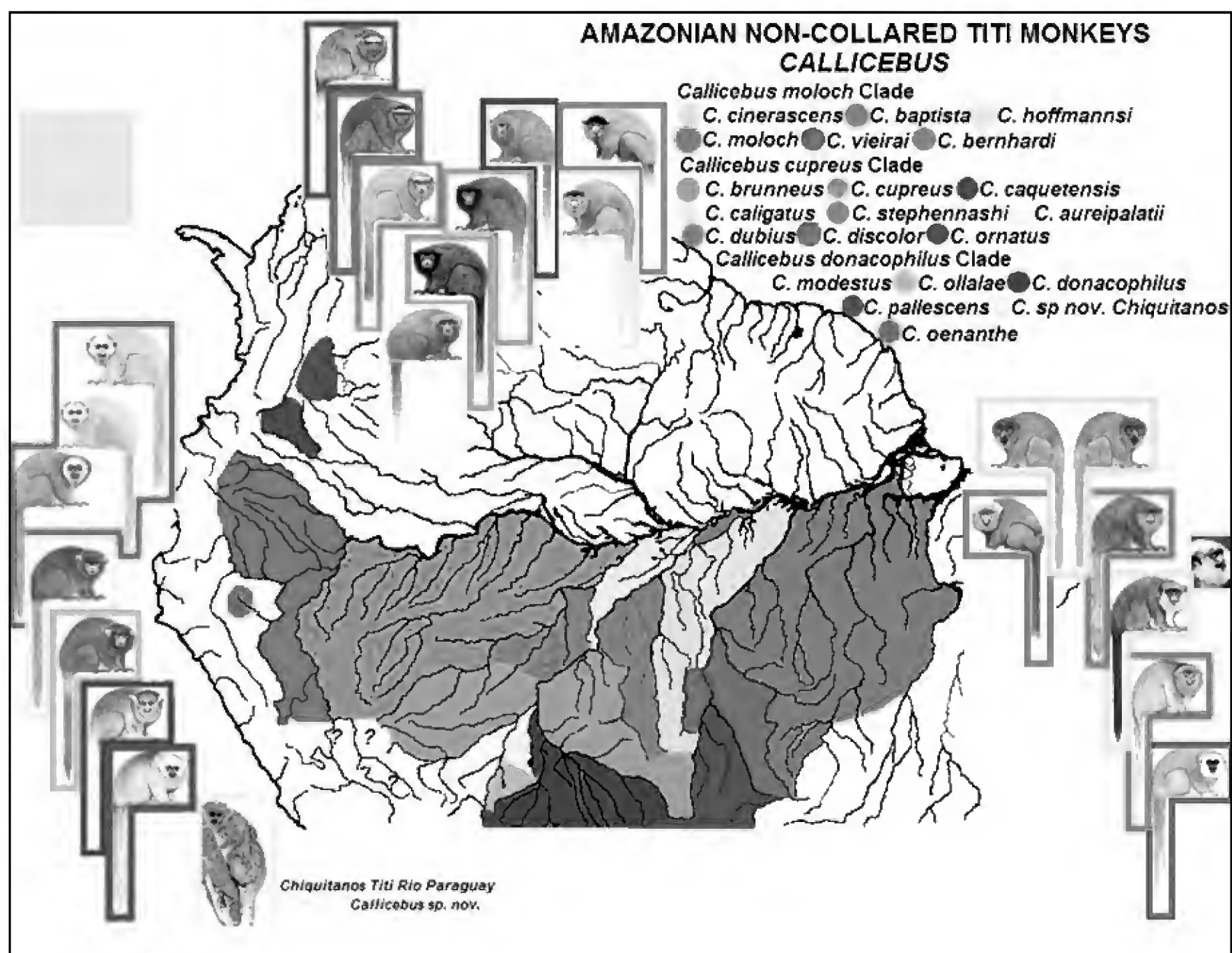


Figure 17. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Amazonian Non-collared Titi Monkeys genus *Callicebus*.

graphy, physiology and behaviour - contributing to test the hypothesis that a certain organism is a species distinct from another. Distinct in what sense? An individual is distinct, a population is distinct, but when and in what way is it a distinct species?

Among the Titi Monkeys of the *Cal. moloch* cladistic Group (Fig. 17), the all-agouti dark-tailed taxon *Cal. cinerascens*, ranging along the east bank of the Rio Aripuanã and between the right bank of the lower Rio Madeira and the left bank of the Rio Canumã, seems to represent the nearest to archetypic, most original or ancestral titi from which all other taxa of the *Cal. moloch* Group have derived. Phylogeographically, the current central-southern Amazonian distribution of *Cal. cinerascens* is thought to represent the center of dispersion of the *Cal. moloch* Clade. In other words, the upper Aripuanã region in Rondonia may be considered the

cradle of *Cal. moloch* Clade's evolution and dispersion. From there, all taxa of the *Cal. moloch* Clade have diverged, radiating away in all (but southern) directions. A distinct metachromic trend to saturated pheomelanin (orange beard and sideburns) and albinotic (cream to white beard, sideburns, tail and/or whole body) can be seen, which means that the most progressively bleached taxa that demographically radiated the farthest away from the archetype's origin of dispersion tend to euchromic or albinotic (i.e., *Cal. moloch* east of the Rio Tapajós, and *Cal. hoffmannsi* in the northernmost dead-end distribution delineated by the untraversable Amazon and Tapajós Rivers). The supposed metachromic pathway taken is as follows: *Cal. cinerascens* radiated first in northern direction, some founder-colony traversed the Paran  do Urari , followed the pheomelanin pathway, and diverged



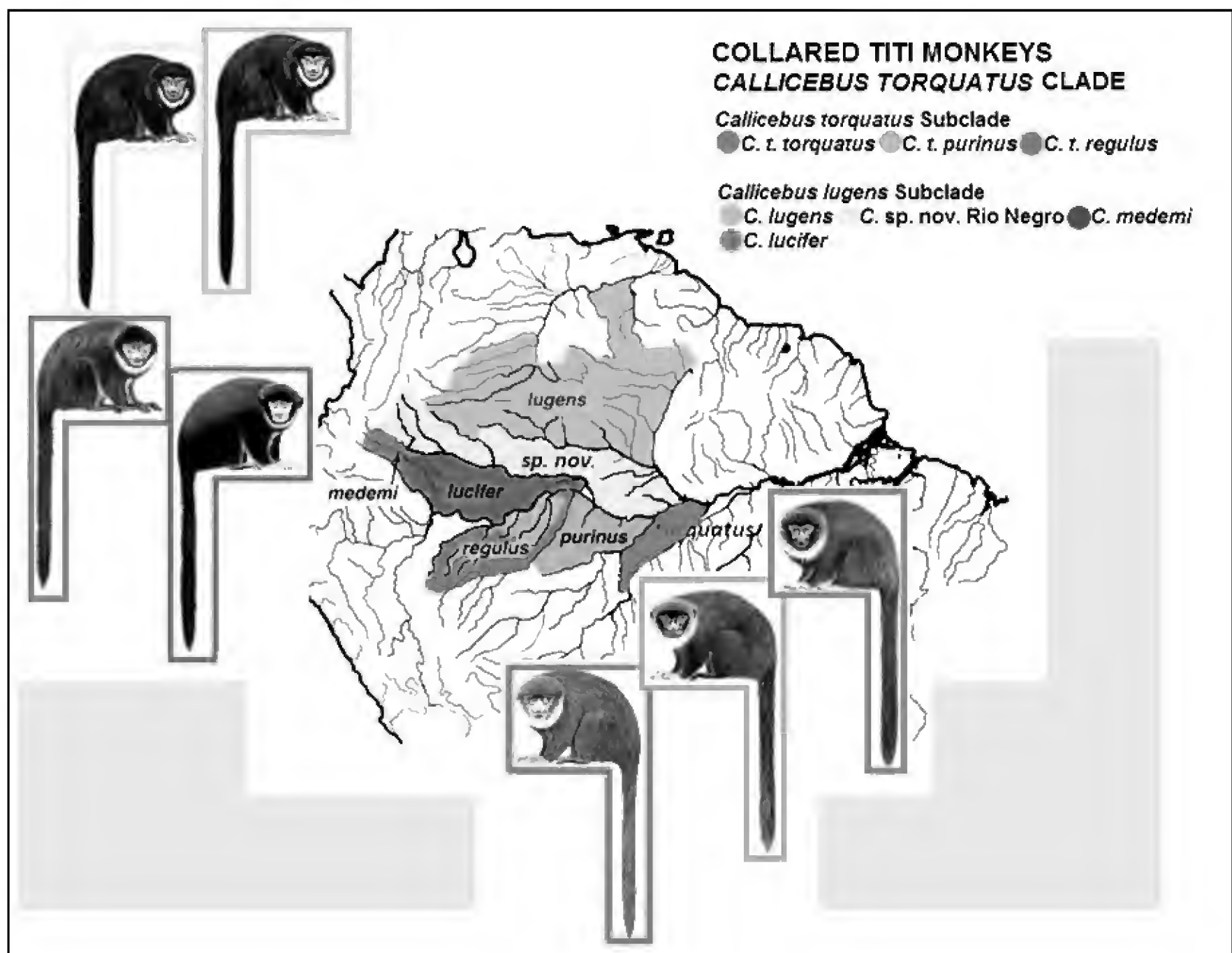


Figure 18. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Amazonian Collared Titi Monkeys of the *Callicebus torquatus* Clade with two sub-Clades: *Cal. torquatus* and *Cal. lugens*.

into taxon *Cal. baptista* (which has dark orange-colored beard, sideburns, lower extremities, and belly). Radiating eastwards, it diverged into *Cal. hoffmannsi* (its forehead, beard, sideburns, hands, feet, and belly bleached light gray to cream-white). After *Cal. hoffmannsi* happened to traverse the Rio Tapajós, most likely where it is called Rio Juruena, it diverged into the advanced pheomelanin bleached to albinotic taxon *Cal. moloch* that now occupies a large distribution east of the Rio Tapajós and south of the Amazon River. *Callicebus hoffmannsi* also diverged along the upper course of the Rio Tapajós into the recently described taxon *Cal. vieirai* (ranging between the Rios Juruena and Teles Pires), which is near-albinotic.

When a taxon is occupying a given interfluvial distribution delineated by hard to traverse river barriers, it has irreversibly changed its pelage or parts of its coat (e.g., beard, sideburns, ear-tufts,

forehead, tail, hands, feet) following the eumelanin pathway from agouti or saturated eumelanin to albinotic (cream or white), via black, brown, drab, and gray, and/or the pheomelanin pathway via red, orange, and yellow, or a combination of the two pathways in different parts of the body or coat. The trend to albinotic in the *Cal. moloch* Clade is completed near its northernmost dead-end distribution in the all-cream to white new form that we happened to identify along the right bank of the Rio Mamurú (Fig. 21). It must have derived from dark-tailed but cream-bearded and -bellied *Cal. hoffmannsi*. Following the trend to allopatry, this color morph (or ecospecies or 'taxon in the making'?) is pushed with the back against the várzeas (white-water floodplain forests) and right bank of the untraversable Rio Amazonas. *Callicebus moloch* Clade's westernmost distribution is represented by the advanced pheomelanin bleached (bright orange

belly, beard and sideburns) to albinotic (white forehead, hands, feet and tail tip) taxon *Cal. bernhardi* which, in turn, is pushed with the back against the also untraversable Madeira River.

Among the Titi Monkeys of the *Cal. cupreus* cladistic Group (Fig. 22), we consider *Cal. brunneus* the nearest to archetypic taxon. Centrally distributed, the overall agouti colored taxon *Cal. brunneus* radiated in northwestern direction via the

progressively pheomelanin bleached taxa *Cal. dubius* and *Cal. discolor* into the most pheomelanin bleached (light orange tail base, beard, sideburns, belly and inner limbs) to albinotic (snow white tail, hands, feet and front/blaze) white-fronted taxon *Cal. ornatus* that is distributed north of the Amazon in the Colombian Amazon. From *Cal. brunneus* southwards diverged the advanced pheomelanin bleached taxon *Cal. aureipalatii* in the Clade's

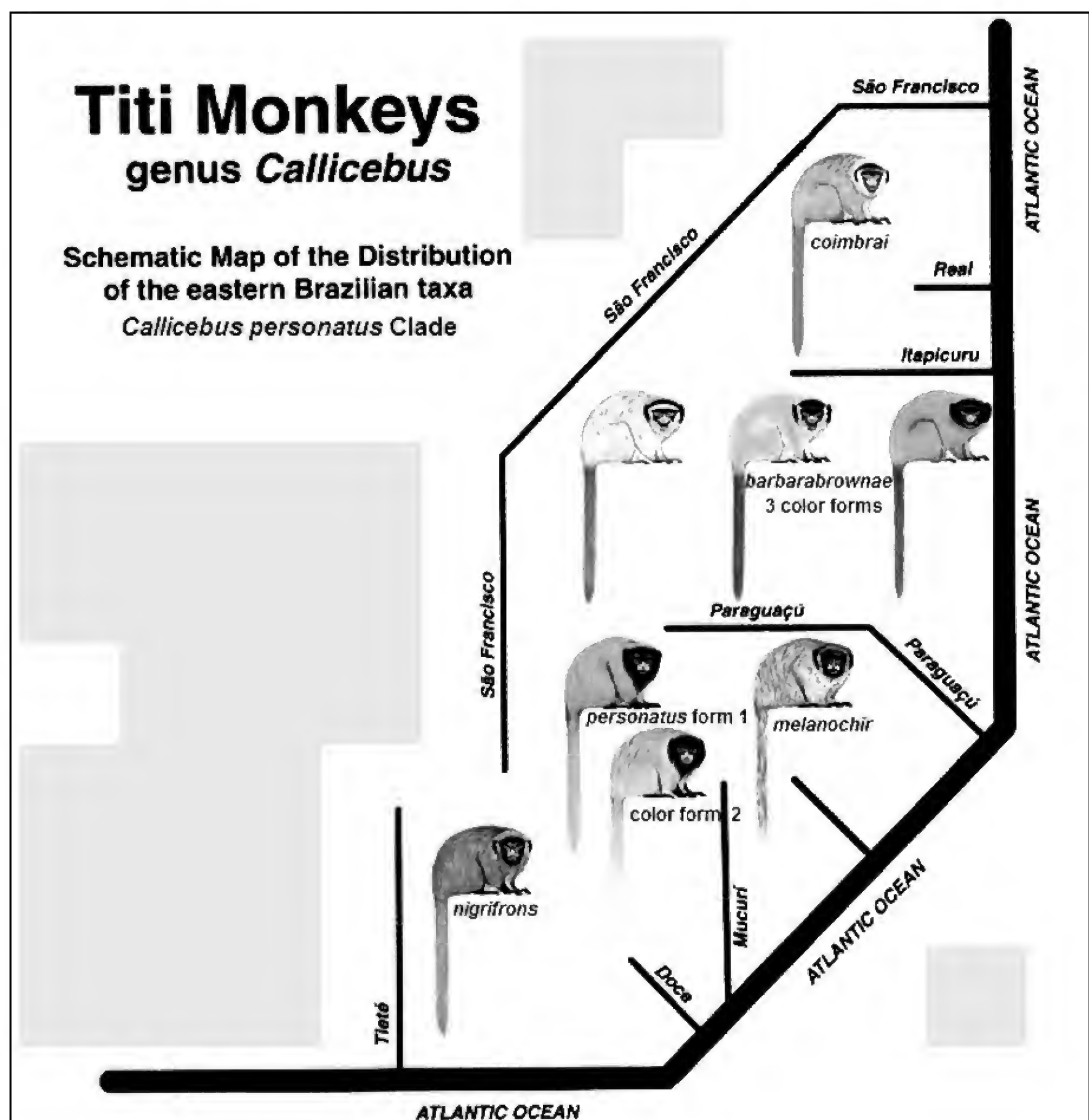


Figure 19. Schematic map of the distributions of the SE Brazilian or Atlantic Forest Titi Monkeys of the *Callicebus personatus* Clade, which are separated by (for these taxa) untraversable rivers.

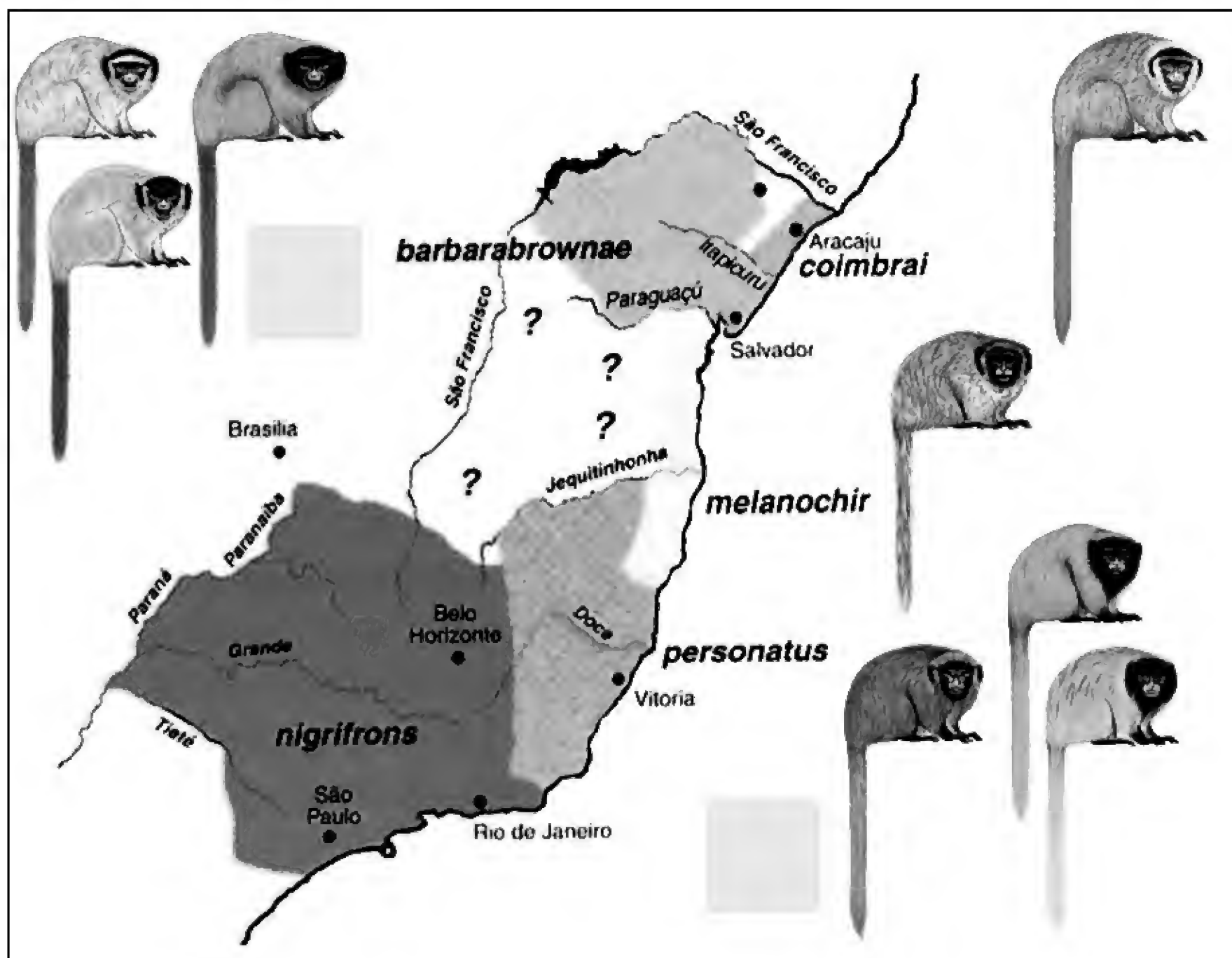


Figure 20. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known SE Brazilian or Atlantic Forest Titi Monkeys of the *Callicebus personatus* Clade.

southernmost distribution (the Bolivian Amazon between the Rios Madre de Dios and Beni). From *Cal. brunneus* radiated away in northern direction first the slightly pheomelanin bleached taxon *Cal. cupreus* that now occupies a large interfluvial area west of the Rio Purús and south of the Rio Solimões. After an ancestral founder-colony of *Cal. cupreus* managed to traverse the Rio Purús to the east, it diverged into the advanced pheomelanin bleached all-orange, but white-tailed taxa *Cal. caligatus* and *Cal. stephennashi* in the northeasternmost dead-end part of *Cal. cupreus* Group's distribution, as the Rio Madeira represents the second strongest riverine barrier on the South-American continent. Last but not least, also from *Cal. cupreus* derived in northwestern direction the recently described, advanced pheomelanin bleached taxon *Cal. caquetensis* that at present occupies

a small, not yet fully identified area north of the Amazon and Caquetá Rivers in the Colombian lowland Amazon, allopatric with and south of the distribution of the white-fronted titi *Cal. ornatus* (Fig. 17).

Among the Titi Monkeys of the *Cal. donacophilus* cladistic Group (Fig. 17), we consider the overall agouti-colored taxon *Cal. modestus* the most original, nearest to archetypic taxon. It occupies the Clade's northernmost distribution delineated by the Rios Beni and Mamoré. It radiated southwards into the slightly pheomelanin bleached orange-brown taxon *ollalae*. Following a eumelanin bleaching pathway, *Cal. modestus* also radiated in southeastern direction, first into the near-albinotic taxon *Cal. donacophilus*, and from there into the fully albinotic taxon *Cal. pallescens*. The latter nowadays occupies the southernmost dead-end

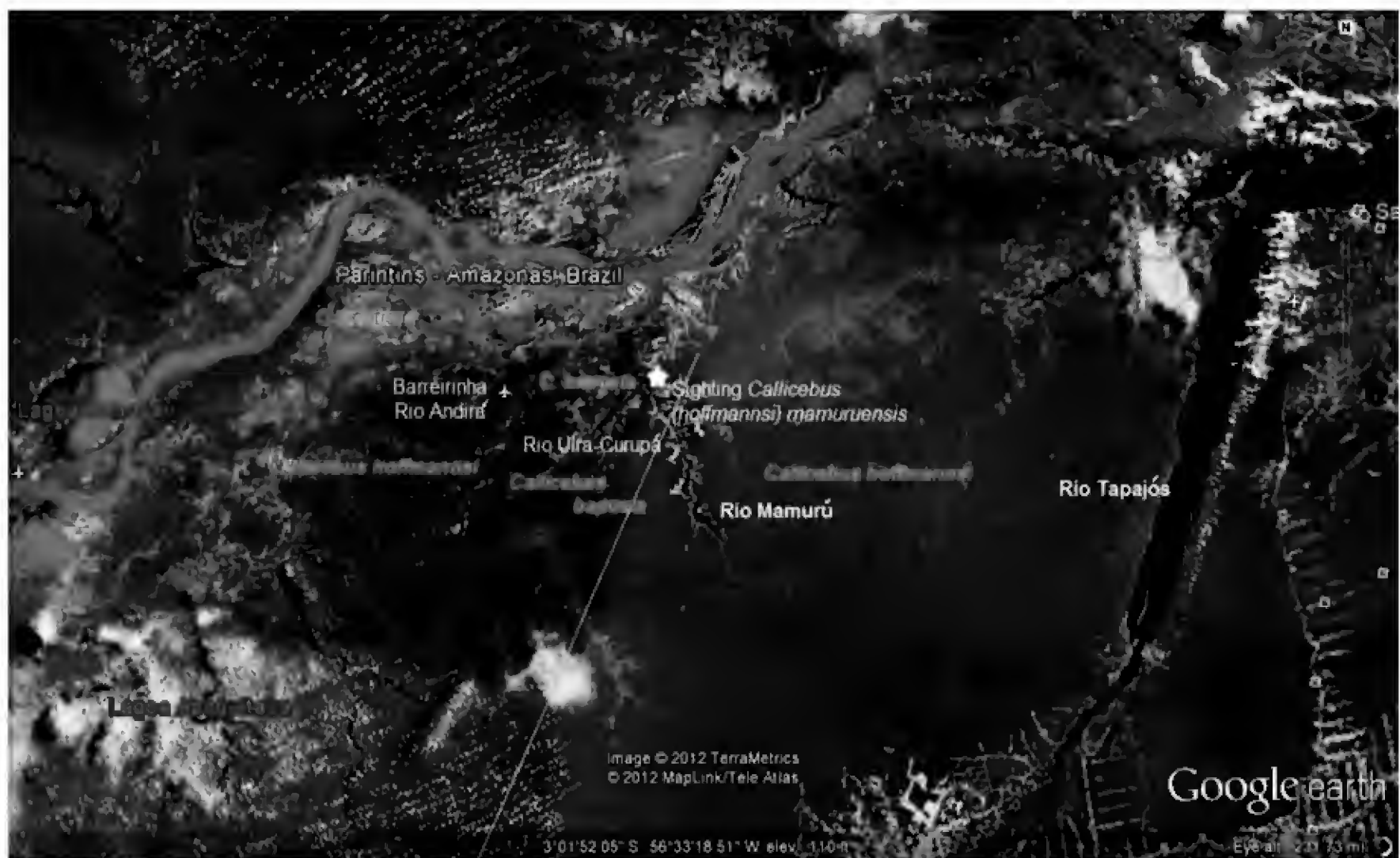


Figure 2I. Distributions of *Callicebus baptista*, *Ca. hoffmannsi*, and the “Rio Mamurú titi” - the latter perhaps to be considered a new taxon or one ‘in the making’. This satellite image shows the location of an enclave population of fully albinotic titi monkeys that we have found to exist along the right bank of the Rio Mamurú. This population is on the verge of extinction as it is pushed with the back against for titis inhospitable habitat - the seasonally inundated floodplain forest (várzea) along the Rio Amazonas and the outskirts of the rapidly expanding town of Parintins in the north, and lands occupied by *Ca. hoffmannsi* stretching to the east as far as the Rio Tapajós. The species *Ca. baptista* belonging to the *Ca. moloch* Clade originally ranged only north of Paran do Canum, P. do Urari and P. do Ramos, east of the lower Rio Madeira, south of the Rio Amazonas and west of the Paran do Ramos. South of this narrow distribution evolved the species *Ca. hoffmannsi*, which occupies a large distribution between Rio Canum in the west, Rio Tapajs in the east, and Rio Amazonas in the north, east of Paran do Ramos and Rio Mamur. Baptist’s Titi is much more colorful being dark to bright red on the ventral parts and lower limbs, having a red beard and red sideburns, whereas the rest of its body is grayish to blackish agouti. Hoffmann’s Titi is basically two-colored grayish and yellowish-white to almost white, its sideburns and beard being light cream-white. However, we spotted the *Ca. baptista* titis also along the west bank of the Rio Ura-Curup, hence it once must have traversed the Paran do Ramos west of the town of Parintins, forming an enclave population there after it displaced Hoffmann’s titis from the interfluv delineated by the lower Rio Ura-Curup and Rio Andir. We also spotted advanced metachromic bleached, near-albinotic, pale yellowish to all-white ‘color morphs’ being phenotypically most related to *Ca. hoffmannsi* along the Rio Mamur, the next river to the east, and classic yellowish-white and gray *Ca. hoffmannsi* with black tails along both banks of the middle and upper Rio Andir. These observations may confirm a case of what is called parapatry. The two valid species *Ca. hoffmannsi* and *Ca. baptista* that are allopatric for the greater part of their distributions - phylogeographically separated from one another by untraversable water bodies - exclude one another where *Ca. baptista* happened to traverse a riverine barrier and subsequently replaced the local *Ca. hoffmannsi* population. There, both taxa live parapatric, meaning in adjacent ‘patrias’ not separated by geographic barriers, where gene flow in theory is possible, but in reality does not occur. A plausible explanation would be that the two taxa have already diverged too far from one another. One could only speculate about the future of the fully albinotic form seen along the right bank of the Rio Mamur. It may represent a founder-colony or population of metachromic progressively bleached individuals that have been driven into parapatry by the *Ca. hoffmannsi* populations found to the east and south of Rio Mamur as far as the Rio Tapajs. The Rio Mamur titis eventually might go extinct, unless they manage to adapt to (for titis) inappropriate habitat - the extensive vrzas along the right bank of the Rio Amazonas. If the founder-colony, following the trend to allopatry, would successfully adapt to the ecological niche of vrzea, then a new taxon could derive from *Ca. hoffmannsi*. Through inbreeding, the currently adopted euchromic coat coloration would stabilize phenotypically across the entire population of that new taxon in a relatively short period of time. The hypothetical evolutionary path would then go from a metachromic fully bleached, near-albinotic color morph in a dead-end distribution to a new taxon belonging to the monophyletic *Ca. moloch* Clade. In that case, we would have to name the Rio Mamur Titi Monkey *Ca. mamuruensis*.

distribution of the *Cal. donacophilus* Clade, penetrating far into the arid Chaco of Paraguay and the pampas of Argentina. A new species of titi, recently collected by the Brazilian ornithologist Marcelo Vasconcellos in the Chiquitanos area along the Rio Paraguay in the Pantanal of Mato Grosso do Sul (for which taxon we identified the holotype in the zoological collection of the AMNH, in 1977 collected by George Schaller and misidentified as *Cal. donacophilus*), represents the easternmost distributed taxon of the *Cal. donacophilus* Clade. Except for its dark gray ears (white in *Cal. donacophilus*), the Chiquitanos titi is overall more pheomelanin bleached towards albinotic than *Cal. donacophilus*, but less so compared to *Cal. pallescens*. Furthermore, from *Cal. modestus* derived in northwestern direction the advanced pheomelanin bleached near-albinotic taxon *Cal. oenanthe* that is nowadays found isolated in a small area in the east-Peruvian Amazon, south of the Río Marañón.

Among the Collared Titis of the *Cal. torquatus* cladistic Group (Fig. 18), we consider the saturated eumelanin black-handed taxon *Cal. medemi* with the westernmost distribution north of the Amazon River the nearest to archetypic form from which derived the all-black but yellow-handed titi from the southbank of the Rio Negro - a newly identified, as yet to be described taxon - and from that taxon derived the all-black, dorsally slightly reddish-tinged taxon *Cal. lugens* with the northernmost distribution of the *Cal. lugens* sub-Clade. From archetypic *Cal. medemi* south of the Rio Caquetá derived, first in eastern direction the dorsally pheomelanin bleached taxon *Cal. lucifer*. Some ancestral founder-colony of the new Rio Negro southbank species then must have managed to traverse the lower Rio Solimões somewhere between the mouth of the Rio Purús and that of the Rio Madeira. From there, collared titis could radiate away back in western direction, though south of the Amazon River, into the further pheomelanin bleached, overall reddish-brown colored white-handed taxa *Cal. torquatus* and *Cal. purinus*, and, after traversing the Rio Juruá, into the advanced pheomelanin bleached red-handed red-fronted taxon *Cal. regulus*.

Within the SE Brazilian Titi Monkeys of the *Cal. personatus* Clade (Figs. 19–20) the nearest to archetypic, most saturated eumelanin taxon is *Ca. melanochir*. It ranges along the Atlantic coast south

of the Rio Paraguaçu in the center of dispersion of the personatus Clade. From *Cal. melanochir* derived in northern direction along the pheomelanin pathway the advanced pheomelanin bleached (all-orange colored) taxon *Cal. barbarabrownae*, and, in a small dead-end distribution delineated by the untraversable lower Rio São Francisco in the north and the Atlantic Ocean in the east derived the almost fully bleached, near-albinotic taxon *Cal. coimbrai*. Radiating in southern direction, ancestral *Cal. melanochir* diverged along the eumelanin pathway into the orange-tailed, but overall dark brown-colored taxon *Cal. nigrifrons*, and along the pheomelanin pathway into the advanced pheomelanin bleached, all-orange colored and near-albinotic taxon *Cal. personatus*.

Within the Squirrel Monkeys genus *Saimiri* (Fig. 22), we phylogeographically distinguish two monophyletic Clades: *Sa. sciureus* - including the Central-American *Sa. oerstedii* sub-Clade - and *Sa. boliviensis* - including the Bare - ear *Sa. ustus* sub-Clade (Hershkovitz, 1984). It is inferred that the genus *Saimiri* evolved relatively recently, with crown lineages diverging as late as the Pleistocene (ca. 1.5 MYA) and other major Clades diverging between 0.9–1.1 MYA. Concurring with Chiou et al. (2011), we include *Sa. oerstedii* in the monophyletic *Sa. sciureus* Clade that originated in the Guianas. North of the Amazon, it radiated in western direction and diverged first into *Sa. cassiquiarensis*, a taxon that is nowadays distributed across the entire Rio Negro basin, its distribution in the south delineated by the Rio Japurá/Caquetá and the lower Rio Solimões. From *Sa. cassiquiarensis* diverged in northern direction the advanced bleached, least colorful taxon *Sa. albigena* that ranges allopatric (north of the Río Guaviare) in the southwesternmost part of the Río Orinoco basin. In concurrence with Chiou et al. (2011), who found evidence for monophyly in the *Sa. sciureus* and *Sa. oerstedii* Groups, we suggest that from *Sa. albigena* or some ancestral precursor of it derived and radiated away in northwestern direction the advanced pheomelanin bleached taxa *Sa. oerstedii* and *Sa. citrinellus*. These now range in *Sa. sciureus* Clade's disjunct northwesternmost dead-end distribution - along the Pacific coast of Panama and Costa Rica. Along a different metachromic pathway derived from *Sa. cassiquiarensis* in southern direction the advanced bleached taxon *Sa. macrodon*. Its distri-



bution is delineated by the Ríos Guaviare and Apaporis in Colombia, and the Rio Japurá in Brazil, and south of the Amazon by the upper Río Marañón in the west, and the Rio Juruá in the east. Within its large distribution, *Sa. macrodon* is excluded from the Ríos Huallaga/Ucayali interfluvium in the Peruvian Amazon that is occupied by *Sa. peruviansis*. In the Guianas, *Sa. sciureus* once managed to traverse the lower Amazon River to the south. As it is a riverbank marsh and mangrove forest specialist, *Sa. sciureus* must have colonized the south bank of the Amazon after reaching it on floating islands covered with várzea or mangrove vegetation. From *Sa. sciureus* south of the Amazon subsequently derived the recently described, advanced bleached near-albinotic taxon *Sa. collinsi* that is confined to Marajó Island - the *Sa. sciureus* Clade's easternmost dead-end distribution delineated by the Atlantic Ocean, and the Amazon and Pará Rivers.

The second monophyletic Clade of Squirrel Monkeys, the *Sa. boliviensis* Clade, has originated in the extensive white-water floodplain forest (várzea) near the confluence of the Japurá and Solimões Rivers. The lower Japurá/Solimões interfluvium does not contain any terra firme. It is seasonally flooded over 6–8 months. Here lives the nearest to archetypic, saturated eumelanin taxon of the *Sa. boliviensis* Clade, *Sa. vanzolinii*. It is overall agouti and black colored, representing the only extant squirrel monkey with an all-black tail. A somewhat bleached *Sa. vanzolinii* founder-colony once must have reached (swimming or on a floating várzea island) the south bank of the Rio Solimões east of its confluence with the Rio Juruá. There evolved from it the somewhat pheomelanin bleached, orange to yellowish taxon *Sa. boliviensis*. It then occupied east of the Rio Juruá the entire area delineated by the lower Purús, upper Madeira and Guaporé

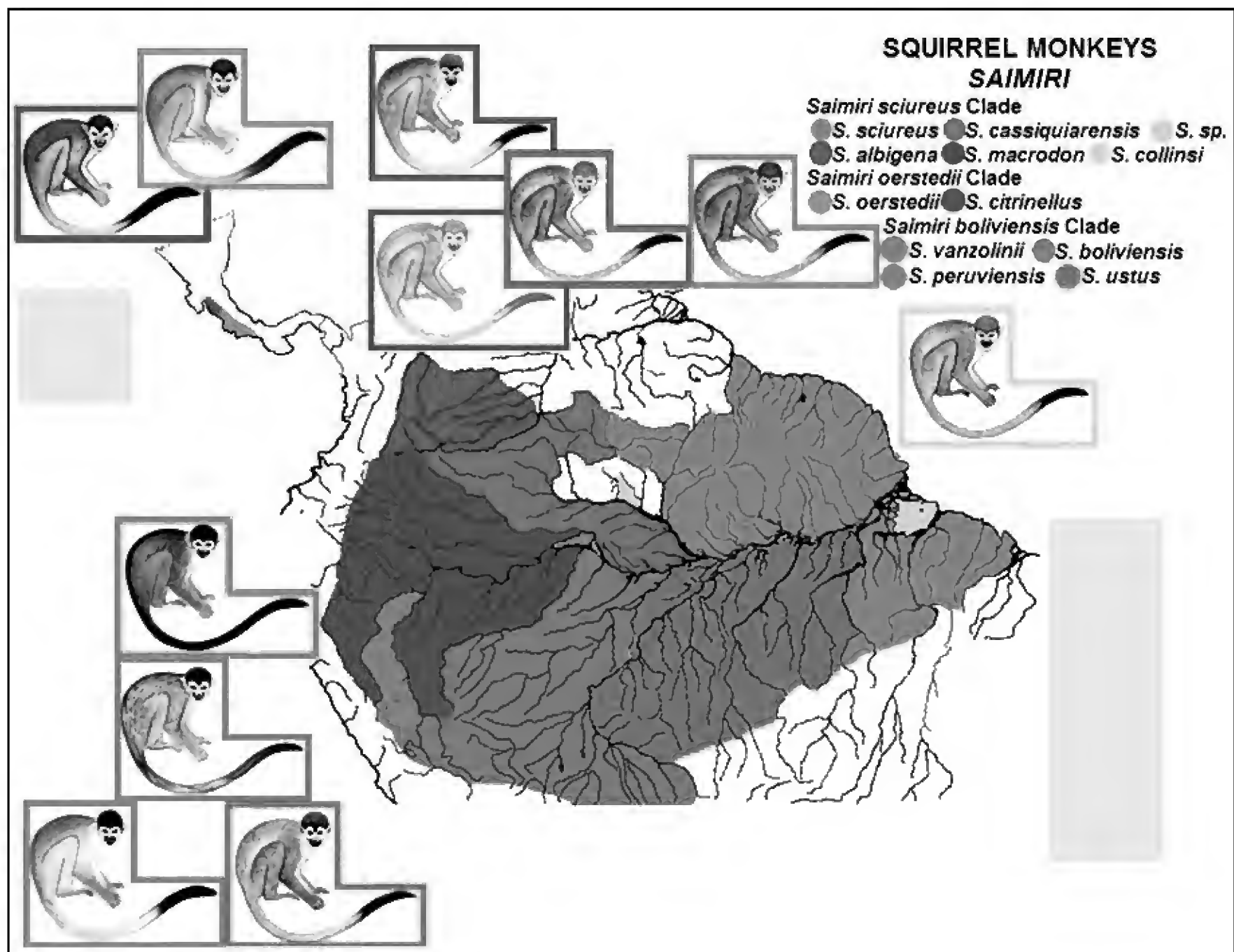


Figure 22. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Squirrel Monkeys genus *Saimiri* divided up in the *S. sciureus* and *S. boliviensis* Clade.

Rivers, whereas in the south it extended its range far into the Peruvian and Bolivian Amazon. After a founder-colony of somewhat bleached *Sa. boliviensis* happened to traverse the easternmost river barrier, it diverged into *Sa. ustus* - the least colorful, most eumelanin bleached taxon of the *Sa. boliviensis* Clade. Its distribution is confined by the Amazon River in the north, the Rio Xingú in the east (separating the distributions of *Sa. ustus* and *Sa. sciureus*), and the Rio Guaporé in the south. Furthermore, from *boliviensis* in its southwesternmost distribution in the Peruvian Amazon derived the progressively pheomelanin bleached near-albinotic, most colorful taxon *Sa. peruviansis*. It occupies a dead-end distribution - the interfluvium delineated by the Ríos Huallaga and Ucayali - as it is surrounded by *Sa. macrodon* occupied territory.

Historically followed metachromic and phylogeographic pathways, intraspecifically pushed ahead by the trend to allopatry and the principle of metachromic bleaching, within a genus or monophyletic Group of primates may be traced back most expressively, when we examine the distributions, speciation and radiation of all extant Uakari Monkeys genus *Cacajao* (Figs. 23, 24). This exclusively Amazonian genus contains two monophyletic Groups or Clades: the Black-headed Uakaris of the *Cac. melanocephalus* Group, and the Bald-headed Uakaris of the *Cac. calvus* Group (Hershkovitz, 1987a). Among Uakaris, the supposedly nearest to archetypic (prototypic) ancestral form is represented by the extant Black-headed Uakaris, more in particular by the saturated eumelanin, all-black taxon *Cac. ayresi* - the northeasternmost distributed among all Uakaris.

Uakaris are the only monkeys in the Neotropics that lost a functional tail. All other genera evolved either a long pendulous, short-hairy to bushy tail that is in the first place designed to use for balance while moving through the tree tops; or, a long prehensile tail that is used as a fifth limb during vertical climbing and walking on top of or brachiating underneath twigs and thin branches in the periphery of tree tops (where the fruits are hanging). Only after observing Black-headed Uakaris *Cac. hosomi* in the wild along the Rio Cauaburi and in Pico da Neblina National Park, we came to understand why the region drained by the Rio Negro has to be considered the center of dispersion for all uakaris, in other words the cradle of evolution of the genus

*Cacajao*. Simultaneously, we came to understand the very reason why uakaris have lost a functional tail, whereas in all other canopy-dwelling monkeys from the Amazon it seems to be a fifth limb of vital importance.

Across the entire upper Rio Negro basin the type of vegetation that dominates the landscape is a very impoverished sort of thin-stemmed savanna forest. It stands on poorly drained, highly acidic white-sand soils that are deposited on top of an impermeable, several meters thick layer of coarse rounded pebbles. This type of forest is called "caatinga-do-Rio-Negro", for it resembles much the arid dry seasonally deciduous vegetation in large parts of the Brazilian northeast. It seasonally floods during the long rainy season, but also throughout the year on a daily base during heavy rainstorms. Physiognomically, this forest type resembles two-storey mangrove forest, as most of its trees use pneumatophores (aerial roots) and stilt-roots to cope with frequent flooding conditions. Phytosociologically, the 'caatinga-do-Rio-Negro' is dominated by trees belonging to families like Euphorbiaceae and Apocynaceae, known for their often toxic latex and plant parts, most in particular full-grown seeds. Surprisingly, this forest lacks hemi-epiphytic climbing shrubs, vines, and twiners. Over geological times Black-headed uakaris seem to have co-evolved with this natural environment through specializing themselves in the depredation of immature seeds. From early maturation on, the seeds are often loaded with toxic alkaloids and secondary compounds. Uakaris have guts that are specially adapted to neutralize these toxins. Their canines are oversized and wedge-shaped with razorblade sharp edges, as such adapted to open up the toughest-husked fruits and kernels (endocarps) around. Their incisors are procumbent and used to scoop out the seed content (endosperm) from any endocarp or pericarp. Uakaris are full-fashioned seed predators to such length that, if one offers a uakari a juicy pear or apple, the monkey will instantly bite the pulpy pome in half with its powerful canines. Then, it will pick the tiny seeds from the central part, discard the pulp, and delicately split the tiny seeds one by one with their canines. In the end, it has its procumbent incisors scoop out the endosperm from the seed coat. Black-headed uakaris do occupy very large home ranges. They restlessly travel or forage in very large multi-male dominated

social groups that may contain over two-hundred monkeys. Since their preferred habitat 'caatinga-do-Rio-Negro' basically lacks climbing shrubs, the tree tops are not interlinked by vines, twiners and climbing hemi-epiphytes as they are in primary terra firme rain forest elsewhere in the Amazon. By lack of a walkway through the tree tops, Black-headed uakaris co-evolutionarily have adapted to this ancient impoverished, physiognomically discontinuous and frequently inundated forest type by developing the locomotor pattern of so-called 'vertical clinging and leaping'. A traveling or foraging troop of Black-headed uakaris much resembles Madagascar indris, *Indri indri* (Gmelin, 1788) that also make enormous leaps, catapulting themselves for - and upwards by means of their strong muscular upper legs. Like indris in Madagascar, black-headed uakaris lost most of a functional tail while adapting to this type of locomotion. The few cm long tail provided with a tuft is only used for intragroup communication. Black-headed uakaris can curl it upwards and wave it sideways like dogs would do with a largely amputated tail.

Black-headed uakaris of the species *Cac. hosomi* and *Cac. ayresi*, distributed north of the Rio Negro, east of the Cassiquiare and west of the Rio Demeni, and *Cac. melanocephalus* from south of the Río Orinoco, west of the Cassiquiare and north of the lower Rio Solimões and Rio Japurá/Río Caquetá, have a pitch-black face, a black, forward directed hair-tuft on the forehead, and a short blackish, red or orange-tinged tail. Black-headed uakaris from the Rio Içana basin, being distributed in-between the upper Río Orinoco and the lower Rio Uaupés, show a black upper back and pheomelanin bleached, orange to blond bleached lower back. Perhaps, for that reason they should be taxonomically treated as a valid species (we here suggest *Cac. ouakary*).

The Bald-headed Uakaris of the *Cac. calvus* cladistic Group, which range south of the Amazon/Solimões and Japurá Rivers, have a bald head, bright-red bare face, blue-gray eyes, a shaggy pheomelanin bleached, near-albinotic coat, and a rudimentary tail that is shorter and even less functional than the tail of Black-headed Uakaris (Figs. 23, 24). The *Cac. calvus* Group contains five taxa which according to our phylogenetic ecospecies concept (ESC) should be all given valid species status: 1) *Cac. calvus* living exclusively in the white-water

floodplain forests (várzeas) between the lower Japurá and Solimões Rivers, being cream-white with pheomelanin bleached, orange-brown ventral parts; 2) *Cac. novaesi* occurring in disjunct pockets along both banks of the lower and middle Rio Juruá as far upstream as its confluence with the Rio Tauruacá, its coat being pheomelanin bleached, orange brown-colored, but albinotic from the back of the head to mid-dorsum; 3) *Cac. rubicundus*, the pheomelanin bleached, bright orange-colored (except for the albinotic cream-white back of the head and neck) bald-headed *Cac. uakaris* that occurs in the white-water floodplain forests (várzeas) along the left bank of the upper Rio Solimões in the central-westernmost Brazilian Amazon; 4) *Cac. ucayalii*, its coat overall saturated pheomelanin, dark brown to orangish colored, ranging in the Peruvian Amazon along the right bank of the Ucayali River in the white-water inundated floodplain forest (várzea) as well as adjacent terra firme rain forest; 5) a form newly identified by us in the year 2000, its coat near-albinotic, advanced euchromic bleached to all-white. We provisionally name this new taxon the "Rio Pauiní Bald-headed Uakari" *Cacajao* sp., for it is only found in the várzeas along the upper Rio Pauiní, a left-bank tributary of the Rio Purús (Figs. 23, 24).

The 'trend to allopatry in metachromic varieties of sociable, but territorial primates' applies to the evolutionary path along which a certain primate race, species, monophyletic clade, or genus has extended its geographic range in the geological past. As a founder - colony or - population at the outer limit of a taxon's current range represents an extremely narrow gene pool, through inbreeding certain phenotypic characters like partial depilation of the skin, or skin/coat coloration will be reinforced in the beginning and therefore advance more rapidly.

Through the process of metachromism (= evolutionary change in tegumentary or hair/skin coloration), with the 'trend to allopatry' in metachromic bleached individuals as the principal behavioral driving force, speciation, radiation, and phylogeography can be plausibly retraced and explained for in all extant Neotropical primates. According to the principle of metachromic bleaching, primate taxa at the base of a phylogenetic tree or clade being the nearest to archetypic, prototypic, primitive, or original, in general are agouti or saturated eumelanin,

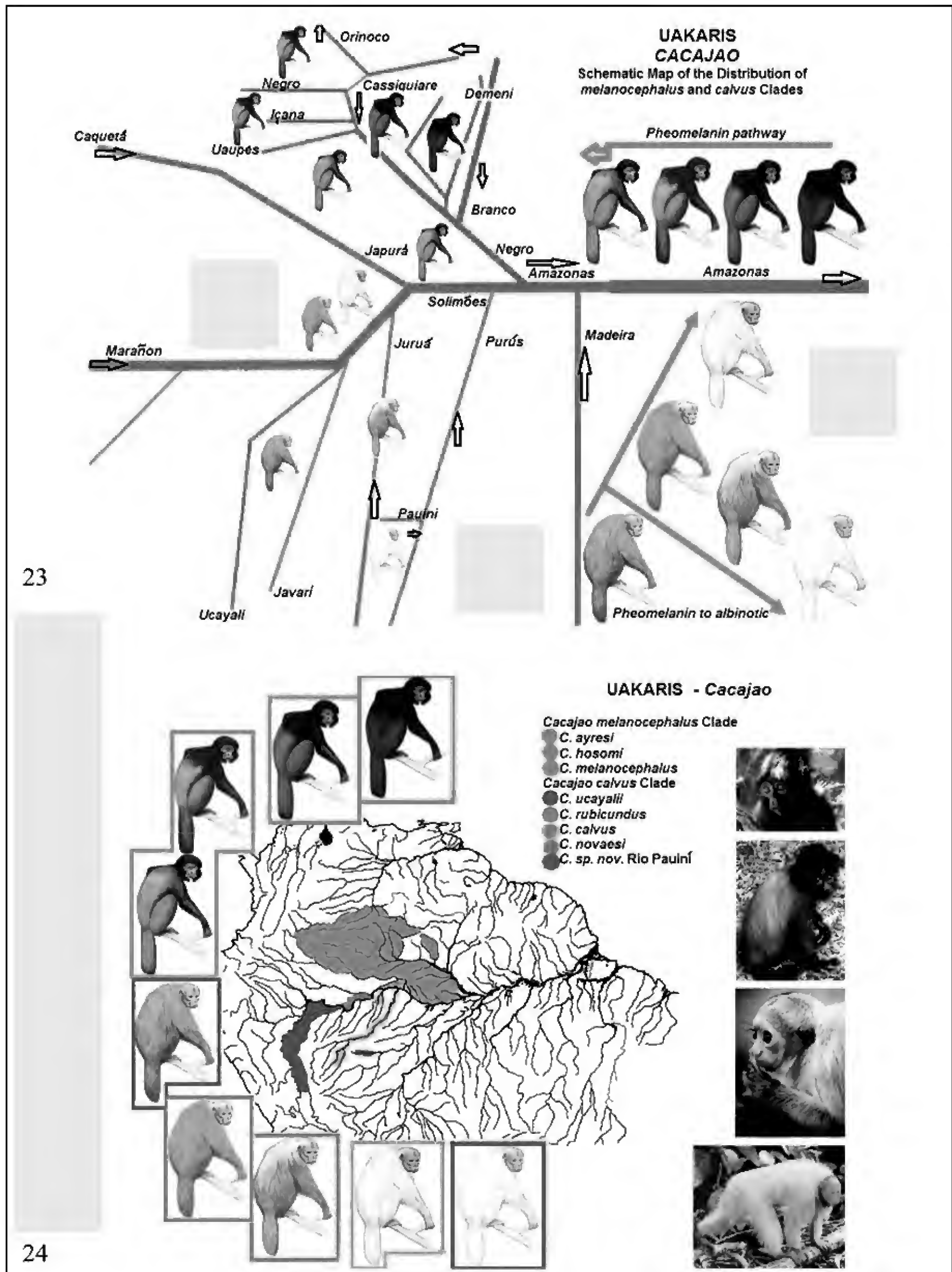


Figure 23. Schematic map of the distributions of Uakari Monkeys of the *Cacajao melanocephalus* and *C. calvus* Clades divided up by (for them) untraversable rivers. Figure 24. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Uakari Monkeys genus *Cacajao*.

which means the least colorful, agouti, black, or dark brown colored. Among Uakari Monkeys genus *Cacajao*, the origin or center of dispersion is supposed to be located in the northeasternmost part of the Brazilian Amazon, south of the watershed between the Rio Negro and Río Orinoco basins, an area delineated by the Rios Demeni and Aracá (Figs. 23, 24; Fig. 27). Within this interfluvium the landscape is dominated by 'caatinga-do-Rio-Negro', the most impoverished habitat type imaginable, but preferred by uakaris of the *Cac. melanocephalus* Clade. Here lives the saturated eumelanin, least bleached taxon of the Black-headed Uakaris, the recently described *Cac. ayresi* (Boubli et al., 2008). Its coat is all-black and dark-brown colored. It may well represent the proto- or archetypic uakari from which all other *uakaris* have derived. From *Cac. ayresi* in western direction first diverged along the pheomelanin pathway taxon *Cac. hosomi*. It is distributed between the Rio Marauíá, the upper Rio Negro, and the Cassiquiare Channel (we have confirmed its presence in Pico da Neblina National Park and along both banks of the Rio Cauaburí). After an ancestral founder-colony traversed the Rio Cassiquiare - the channel that connects the Rio Negro basin with that of the Río Orinoco in Venezuela - *Cac. hosomi* diverged into an intermediately pheomelanin bleached taxon that differs from classic *Cac. melanocephalus* in the black shoulders, dark-red legs and tail. If this phenotype, which is thought to represent a color morph of *Cac. melanocephalus*, turns out to occur throughout the entire distribution delineated in the north by the Río Orinoco and in the south by the Rio Uaupés, one should consider it a new taxon to be named the "Rio Içana Black-headed Uakari" *Cac. ouakary*. After an ancestral founder-colony of the latter managed to traverse the Rio Uaupés, it has diverged into the progressively pheomelanin bleached blond-backed black-headed uakari taxon *Cac. melanocephalus*. Subsequently, blond-backed *Cac. melanocephalus* have occupied the entire interfluvium south of the Rio Negro, eastwards as far as Archipelago de Anavilhanas located about forty km west of Manaus, and to the west far into the Colombian Amazon, and south as far as the north bank of the Rio Japurá (Río Caquetá in Colombia). We suppose that once upon a time a founder-colony of slightly bald-headed, advanced pheomelanin bleached ancestral *Cac. melanocephalus*, being

pushed out of its westernmost dead-end distribution in the Colombian Amazon, may have managed to traverse the upper reaches of the Río Caquetá. It then could extend its range southwards, eventually reaching the Río Marañón (as the upper Amazon River is called in Peru). A founder - colony of an advanced pheomelanin bleached, bald-headed ancestral form must then have traversed the Río Ucayali. It subsequently occupied terra firme and várzea forests in the interfluvium between the Río Ucayali in the west, the Río Marañón in the north, and the Rio Javarí in the east. Nowadays, this interfluvium is inhabited by the bald-headed dark reddish-brown taxon *Cac. ucayalii* that belongs to the bald-headed *Cac. calvus* Clade. Disjunct from *Cac. ucayalii*'s distribution and ranging farther to the east derived taxon *Cac. rubicundus*, a progressively pheomelanin bleached bright-orange colored bald-headed uakari. It is fully adapted to várzea habitat found in abundance along the left bank of the upper Rio Solimões. From *Cac. rubicundus* going farther eastwards, but disjunct from its distribution, along the same (left) bank of the Solimões/Amazon River the almost fully albinotic taxon *Cac. calvus* is found. It is fully adapted to white - water inundated floodplain forest (várzea) - the only available habitat in this for the *Cac. calvus* Clade dead-end distribution situated inbetween the banks of the Japurá and Solimões Rivers. Directly from *Cac. rubicundus* to the south of *Cac. calvus*' distribution derived the bald-headed taxon *Cac. novaesi* that ranges along both banks of the Rio Juruá as far south as the confluence with the Rio Tarauacá and Rio Envira. This taxon is near-albinotic from the back of the head to beyond the mid-dorsum, and progressively pheomelanin bleached light orange-brown on the lateral and ventral parts of the body. It ranges in the várzeas of the floodplain, but we have also spotted large troops foraging for immature seeds in the adjacent terra firme rain forest.

In 2000, we identified a fifth taxon of bald-headed uakari, the completely white, fully albinotic taxon that we named "Rio Pauini Bald-headed Uakari" *Cacajao* sp. It lives along the south bank of the Rio Pauini, a left-bank tributary of the upper Rio Purús. It represents the southernmost distributed and the farthest pheomelanin bleached most albinotic taxon of all extant uakaris. It lacks the pheomelanin orange-brown to orange



ventral parts seen in the other near-albinotic taxa *Cac. novaesi* and *Cac. calvus* (Figs. 23, 24).

Analyzing metachromic skin and coat characters as linear and irreversible progressions within Neotropical primate genera and their monophyletic Clades does add substantially to the reconstruction of biogeographic divergence events and phylogenetic relationships over a wide range of Neotropical primate taxa, in particular those that defend their living space or ecological (feeding) niche through male-dominated, hierarchically organized societies. So it does to the Bearded Sakis genus *Chiropotes* (Figs. 25, 26) even if we have confirmed in the field that social groups of (at least) the Guianan taxon *Ch. sagulatus* do freely fuse and fission on a regular base with neighboring social groups. The genus *Chiropotes* clearly shows sexual dimorphism in the larger, more robust males that also grow bigger beards and frontal hair lobes on their heads (Herskovitz, 1985). During foraging and resting, a large social group of bearded sakis, similar to woolly monkeys, consists of several polygamous dominant males each taking care of his 'harem'. The high-ranking males tend to stick to the center of the foraging troop, whereas lower ranking males with or without harems are pushed closer to the periphery of the foraging troop. This way, adult males do avoid confrontations, for their impressively large wedge-shaped canines designed to crack hard-husked fruits and kernels in order to get to the seed pulp would be lethal if used in fights. But adolescent, subadult, and, we assume, also behaviorally or phenotypically deviant individual males may well be pushed into the periphery of the foraging and ranging troop. More than once, we have encountered a solitary male, or a couple of males traveling at high speed through the canopy in an apparently fixed direction, leaving us no means to determine if these monkeys only temporarily had lost contact with the troop, or if they were expelled from the parental troop, or if they were representing subtly deviant young males that had been forced to leave the pack and search for new living grounds somewhere beyond the limits of the group's home range. Only through long-term field studies one would be able to obtain clear answers to this sort of questions.

Within the Bearded Sakis genus *Chiropotes* we distinguish two monophyletic Groups: the *Ch. satanas* and the monotypic *Ch. albinasus* Group.

The *Ch. satanas* Clade consists of five taxa, among which the nominate species *Ch. satanas* represents the saturated eumelanin, all-black, nearest to archetypic bearded saki. Its distribution in the NE Brazilian state of Maranhão is assumed to represent the cradle of evolution or center of dispersion for the genus. An equally all-black form that we recently identified west of the headwaters of the Rio Xingú (e.g., Rios Ronuro, Batovi and Vonden Steinen) may either represent an enclave population that became disjunct from that of *Ch. satanas* (ranging east of the Rio Pará/lower Rio Tocantins), or a new taxon of the *Ch. satanas* Clade that still has to be collected and described. From *Ch. satanas* diverged in western direction the slightly eumelanin bleached, overall light-brown colored taxon *Ch. utahicki*. It occupies the entire interfluvial delineated by the Rios Amazonas/Anapú/Tocantins-Araguaia/Xingú. An ancestral founder-colony of somewhat pheomelanin bleached, red to orange-brown backed *Ch. utahicki* once must have managed to traverse the lower Rio Amazonas, from which then derived taxon *Ch. sagulatus*. This species occupies the entire area north of the Amazon River and east of the Rio Branco, including most of the Guianas east of the Essequibo River. This taxon is absent from most of Amapá state, French Guiana and also from a wide coastal belt of the Guianas. A founder-colony of ancestral *sagulatus* once must have traversed the Rio Branco and radiated in western direction diverging into the advanced eumelanin bleached taxon *Ch. israelita*. This species is characterized by the albinotic (white instead of pink) genitals and the light-grayish to brownish coat color of the trunk. *Chiropotes israelita* ranges west of the Rio Branco as far north as the Río Orinoco in Venezuela. It seems to be parapatric with Black-headed Uakaris, as *Chiropotes* is a seed-predating terra firme rainforest specialist, and *Cac. ayresi* and *Cac. hosomi* are 'caatinga-do-Rio-Negro'-habitat specialists. The Rios Marauíá and Cauaburí seem to divide their distributions. Our extensive surveys in the Rios Demeni/Aracá interfluvial did not reveal the occurrence of *Ch. israelita*, as the landscape is dominated by 'caatinga-do-Rio-Negro' habitat (Figs. 26, 27).

The second monophyletic Group of Bearded Sakis is that of monotypic *Ch. albinasus*. The Red-nosed Bearded Saki is very different from the *Ch. satanas* Clade, not just in metachromic sense. Its

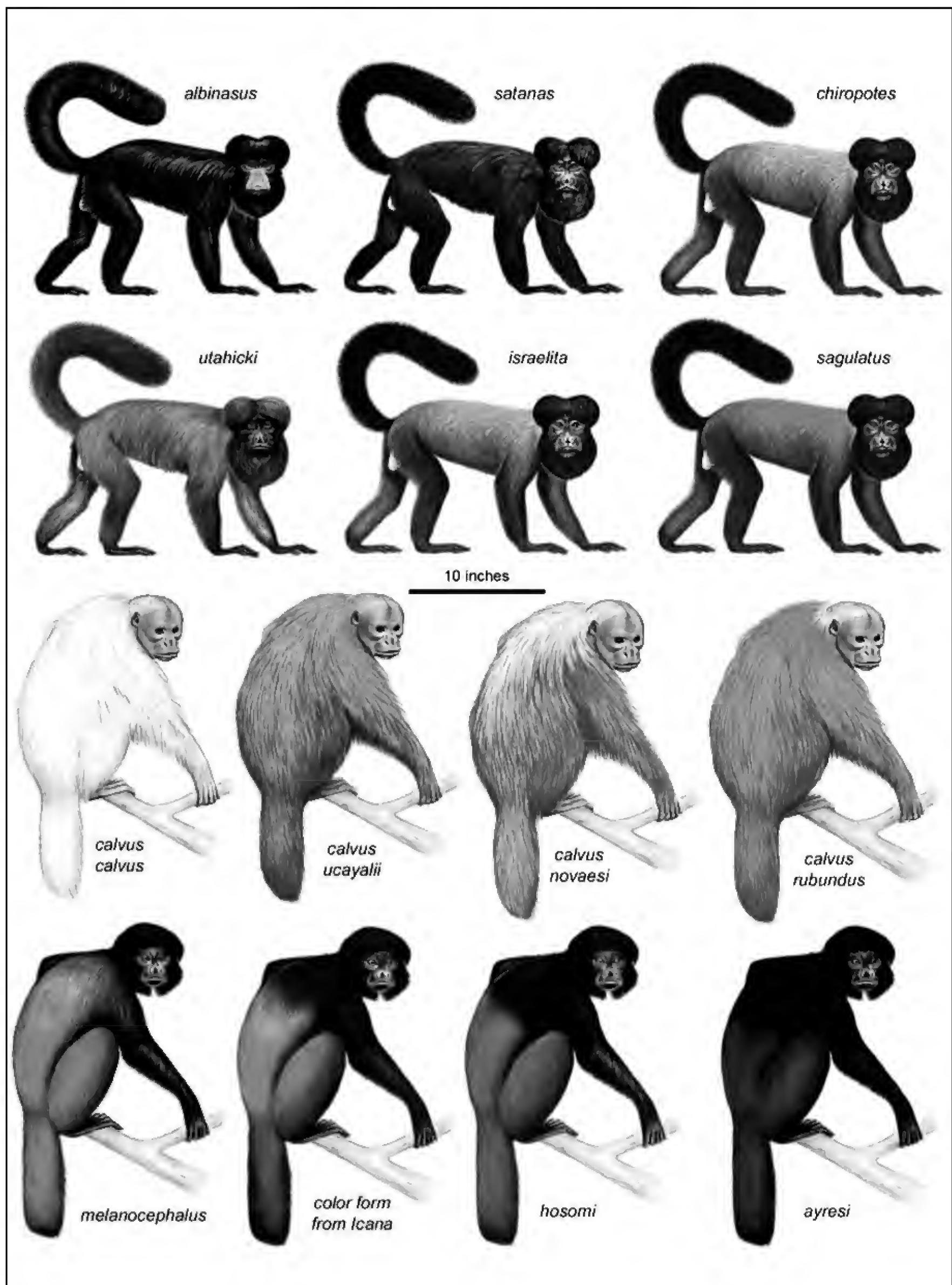


Figure 25. The hitherto recognized taxa of Bearded Sakis genus *Chiropotes* (above) and Uakaris genus *Cacajao* (below), all depicted in one plate (Courtesy of Stephen Nash).

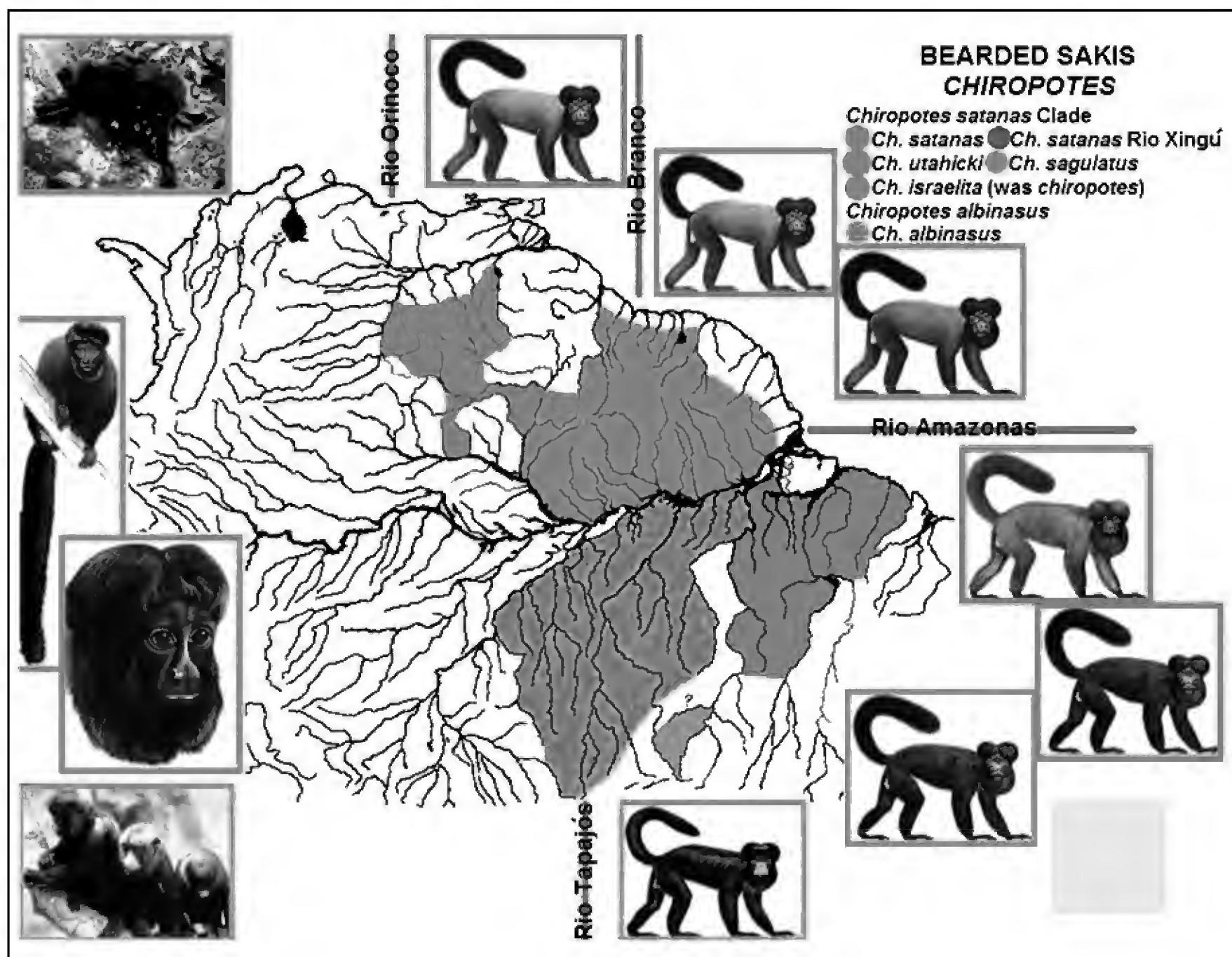


Figure 26. Distributions, allopatric speciation, radiation, and supposedly followed eumelanin pathways of metachromic bleaching in all known Bearded Sakis genus *Chiropotes*.

vocalizations are very different, the beard and tail are shorter-haired, and the genitals of each gender are brightly red-colored as is the muzzle (the scientific name *Ch. albinasus* - Latin for “white nose” - relates to the taxonomist, who may never have seen the monkey he described alive. Furthermore, group size in *Ch. albinasus* is much larger than that of any of the taxa belonging to the *Ch. satanas* Clade, ranging on average from 30–80 individuals. Where *Ch. albinasus* occurs in sympatry with woolly monkeys (i.e., west of the Rio Tapajós-Juruena, east of the Rio Madeira, and north of the Rio Jí-Paraná), they are often seen in mixed species associations. Red-nosed saki groupings mixed with woolly monkeys (*Lagothrix cana*), tufted capuchins (*Sapajus apella*) and/or white-fronted slender capuchins (*Cebus unicolor*) may contain as many as 150 monkeys.

In figure 28, we have depicted the distributions, allopatric speciation, radiation, and supposedly followed pathways of metachromic bleaching in all known Saki Monkeys genus *Pithecia*. Sakis occur exclusively in the rain forests of lowland Amazonia and the Guayanan Shield (Hershkovitz, 1987b; Mittermeier et al., 2013). Within the genus *Pithecia* we distinguish three monophyletic cladistic Groups: *P. monachus*, *P. pithecia*, and *P. hirsuta* (Fig. 29).

Within the *P. monachus* Clade allopatric speciation is thought to have followed evolutionary pathways of metachromic bleaching with *P. monachus* representing the nearest to archetypic precursor of all extant sakis. Both sexes have an overall saturated eumelanin, slightly bleached silky coat, except for the cream-white hands and feet. Taxon *P. monachus* ranges along both sides of the Amazon upstream from its confluence with the Rios Juruá and

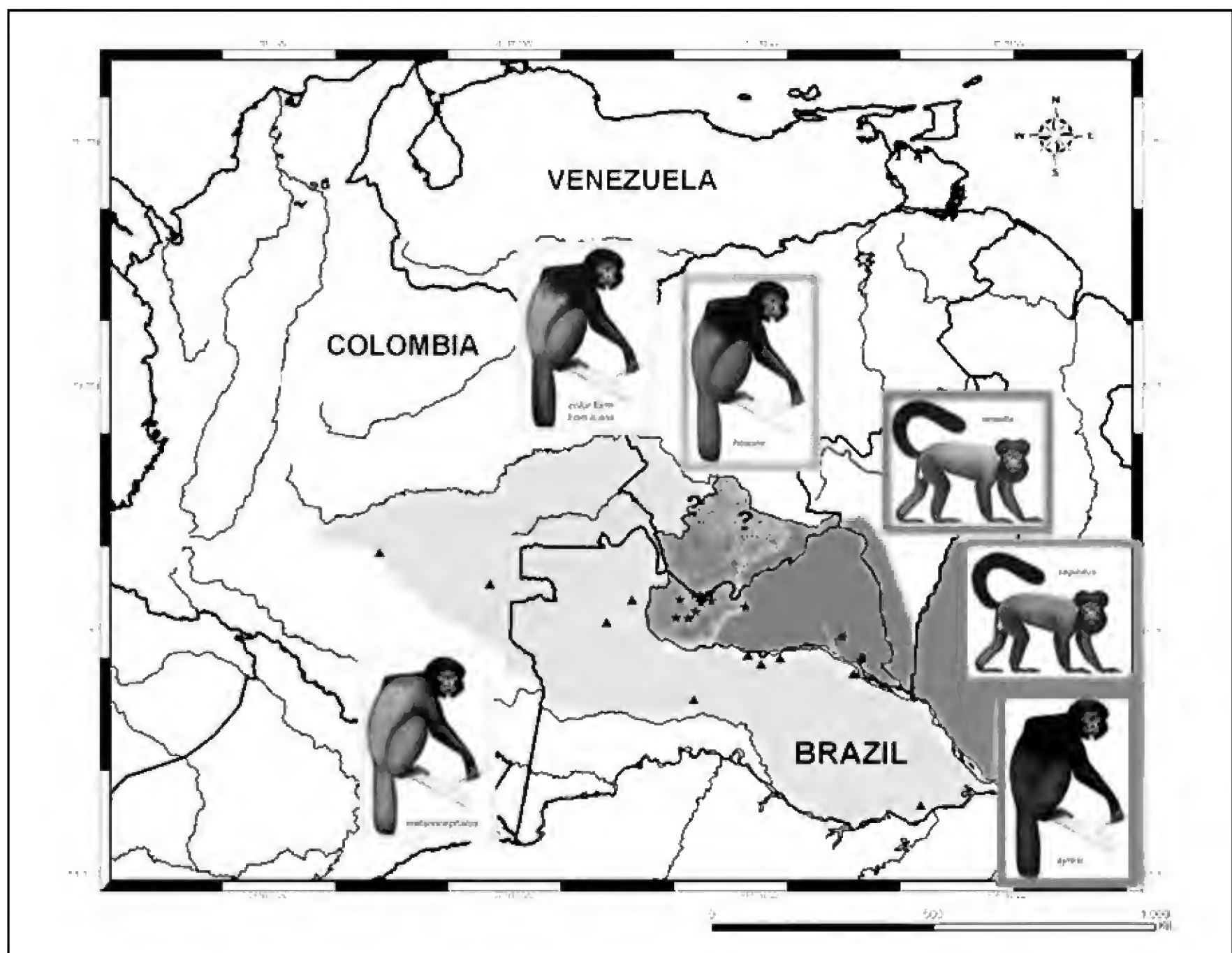


Figure 27. Map showing distributions of the Bearded Saki taxa *Chiropotes sagulatus* and *C. israelita*, and the parapatric Black-headed Uakaris that occur north of the Amazon and Negro Rivers.

Japurá, large rivers delineating its distribution in the east and north. The species is sexually dimorphic, not in size but in metachromic pelage characters of the head. Both sexes have a slightly bleached mask that is light brown in males and cream-white in females. It surrounds a black face with yellow to cream eyebrows and malar stripes. Forehead and cheeks are covered with short, forward directed hairs resembling much that of members of the *P. pithecia* Group. From *P. monachus* diverged in northwestern direction taxon *P. milleri*, supposedly after a metachromic deviant founder-colony of ancestral monachus traversed the Río Caquetá. *Pithecia milleri* nowadays occupies a small part of the Colombian Amazon that is confined by the Ríos Caguán and Putumayo. Both sexes are overall eumelanin bleached, more so in females. The forehead is covered with long, forward directed hairs forming

a kind of hood that is yellowish in males and cream-white in females. The black muzzle is contrasted with the advanced euchromic malar and lip stripes. From *P. milleri* derived the taxon *P. napensis* after a founder-colony of *P. milleri* traversed the Río Putumayo in southern direction. *Pithecia napensis* occupies a small area in the Colombian and Ecuadorian Amazon delineated by the Río Putumayo in the north and the Río Napo in the south. In *P. napensis* both sexes are progressively pheomelanin bleached in the yellowish to orange breast, more so in males that also differ in the silvery grayish lower part of a well-defined mask and in the albinotic hood. After a founder-colony of ancestral *P. napensis* once traversed the Río Napo to the south, the progressively pheomelanin bleached taxon *P. aequatorialis* diverged. It occupies a large area in the Ecuadorian and Peruvian Amazon delin-



eated in the north by the Río Napo and in the south by the Río Tigre. *Pithecia aequatorialis*, in particular in the metachromic characters of the male's head (fully albinotic mask) and (orange) breast pelage, represents the most advanced pheomelanin bleached taxon in the *P. monachus* Clade. Its dead-end distribution at the end of the phylogeographic radiation of the *P. monachus* Clade is confined at all but western (Andean Mountain range) sides by *P. monachus* occupied territory. We may ponder about what would be the result of any hypothetical hybridization between *P. aequatorialis* females and *P. monachus* males at the contact zone that should exist in the species' westernmost distribution. Even if the offspring would remain fertile, it would never result in parapatric speciation. In concurrence with our theory, deviant young males with metachromic genes from *P. aequatorialis* would be expelled by

the dominant male(s) of the *P. monachus* parental group, back to *P. aequatorialis* territory.

Within the *P. pithecia* Clade we consider *P. lotichiusi* with the overall darkest agouti (in females) and saturated eumelanin black (in males) pelage the nearest to archetypic taxon. This taxon is only found in the easternmost part of the interfluvial peninsula between the lower Solimões and Negro Rivers, from opposite the city of Manaus as far west as the towns of Manacapurú and Novo Airão. In the past, *P. lotichiusi* may have occupied a much larger distribution, for no untraversable geographic barriers exist when going further west into the Rios Solimões/Negro interfluve. If so, the *P. pithecia* Clade may have monophyletically derived from the *P. monachus* Clade, when that radiated to the east. A founder-colony of slightly pheomelanin bleached ancestral *P. monachus* may

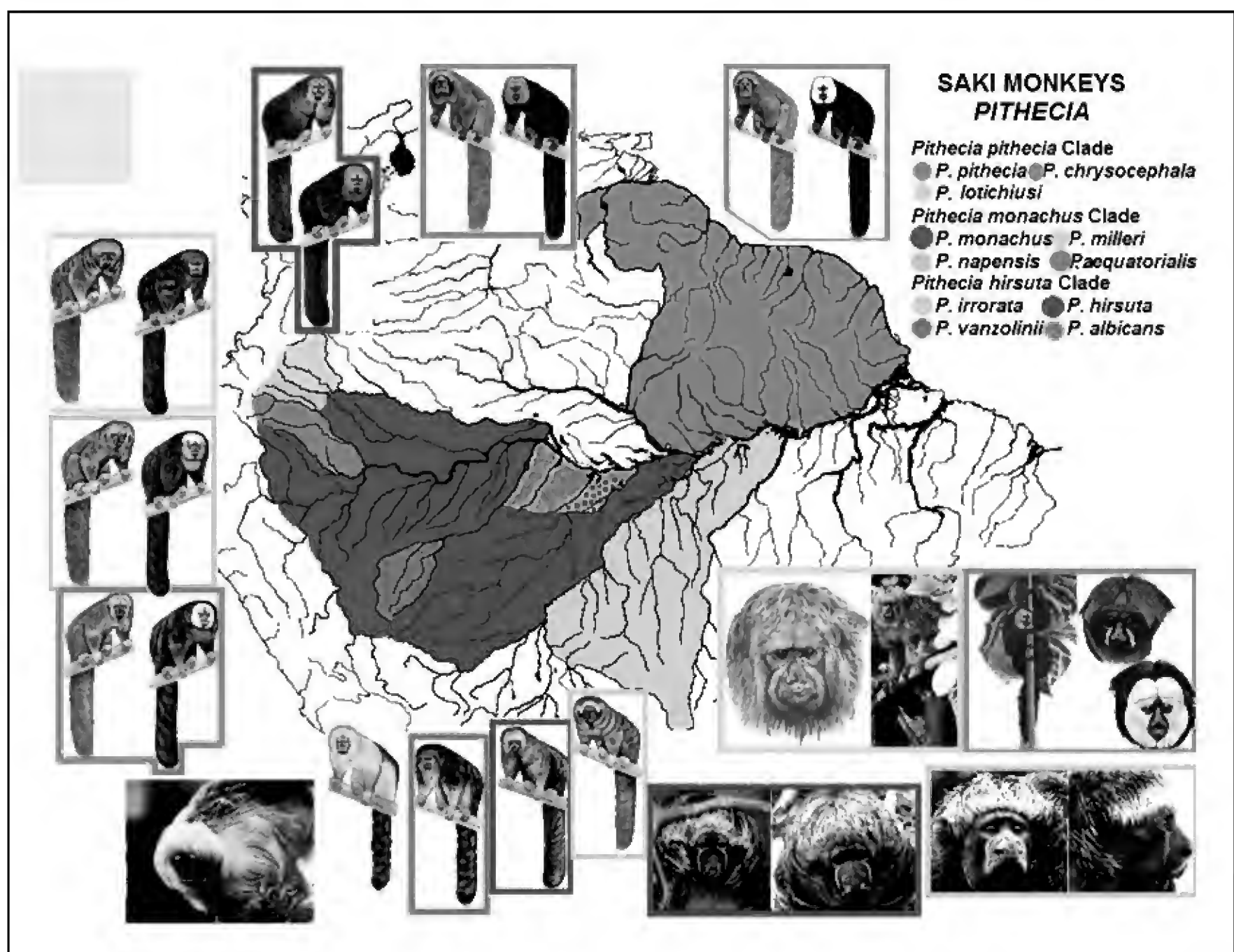


Figure 28. Distributions, allopatric speciation, radiation, and supposedly followed metachromic pathways of bleaching in all known Saki Monkeys genus *Pithecia*.



have traversed the lower Rio Japurá and thereafter diverged into the allopatric taxon *P. lotichiusi*. The latter then extended its range to the east. During one of the late-Pleistocene glacials, when ocean levels dropped over up to 120 m, a founder-colony of *P. lotichiusi* could well have traversed the lower Rio Negro and then reached the north bank of the Amazon. This way, it may have diverged into the allopatric Golden-faced Saki taxon *P. chrysocephala*. Nowadays, Golden-faced sakis range from the Rio Branco as far east as the Rio Trombetas. After a founder-colony of ancestral *P. chrysocephala* once traversed the Rio Trombetas, taxon *P. pithecia* may have diverged. *Pithecia pithecia* then expanded its range in northwestern direction across the states of Roraima, Pará and Amapá, and

across the Guianas into Venezuela as far west as the lower Río Orinoco. It may have circumvented either side of the watershed formed by the Tumac Humac Mountains. Within the sexual dimorphic *P. pithecia* Clade, females are progressively pheomelanin bleached orange to yellowish brown, whereas males are all-black with a progressively pheomelanin bleached to albinotic mask. In the Brazilian taxa *P. lotichiusi* and *P. chrysocephala* the mask that consists of short, stiff, forward directed hairs is golden to orange-yellow colored. In the Guianan white-faced saki *P. pithecia* the mask is albinotic, white with orange-colored cheeks in males from Guyana and Suriname, and overall white in males from French Guiana.

Sakis of the *P. monachus* and *P. pithecia* Clades

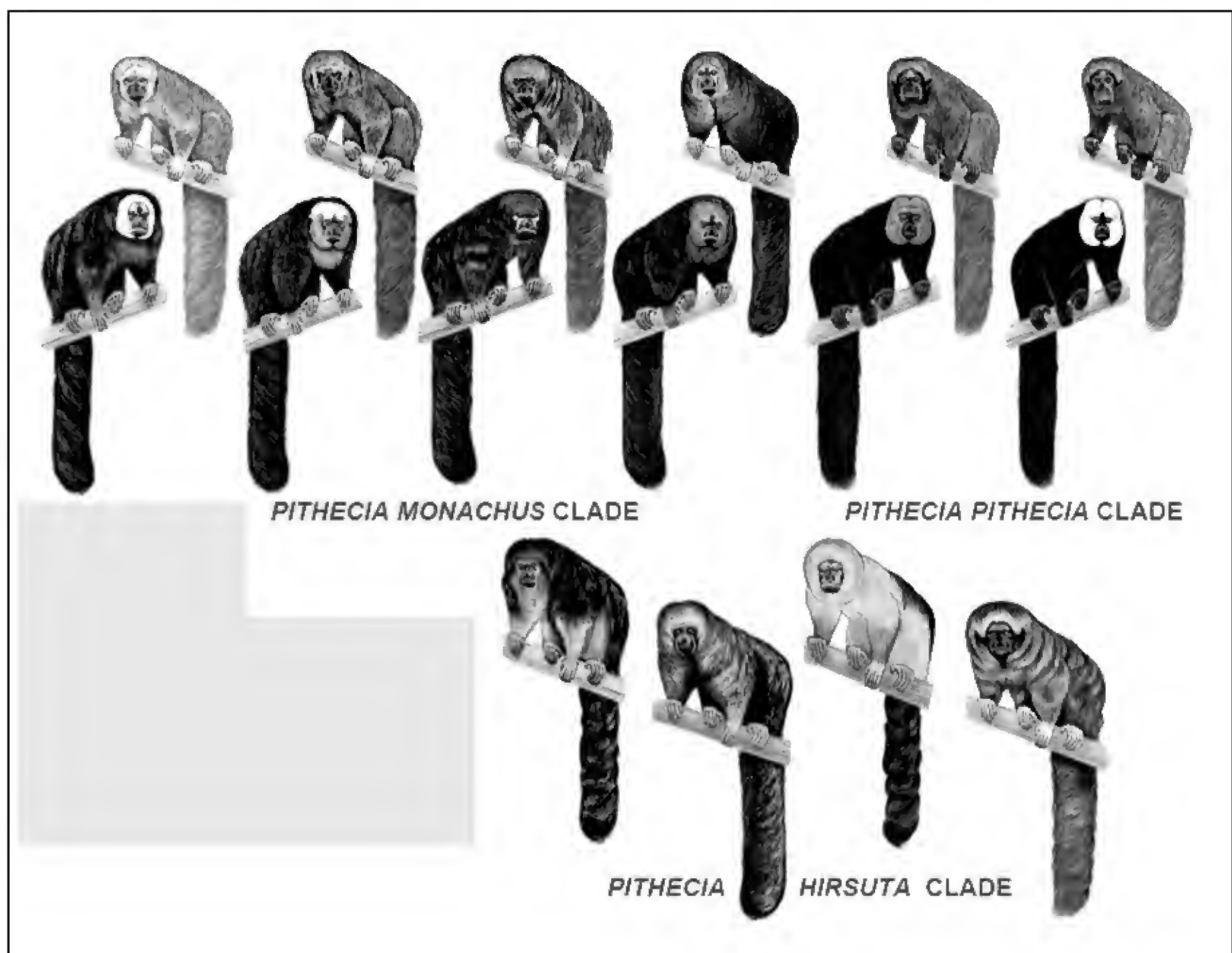


Figure 29. Among the Saki Monkeys genus *Pithecia* three monophyletic cladistic Groups or Clades are distinguished: the *P. monachus* Group containing four taxa (*P. monachus*, *P. milleri*, *P. napensis*, and *P. aequatorialis*), the *P. pithecia* Group containing three taxa (*P. lotichiusi*, *P. chrysocephala*, and *P. pithecia*), and the *P. hirsuta* Group containing four taxa (*P. hirsuta*, *P. irrorata*, *P. vanzolinii*, and *P. albicans*). We only recognize sexual dimorphism as expressed in metachromic characters in the *monachus* and *pithecia* Clades (Courtesy of Stephen Nash).

distinguish themselves locomotorily from sakis of the third clade - the *P. hirsuta* Clade. A specific locomotor pattern called “vertical leaping and clinging” is performed during foraging and traveling in their preferred habitat, which is the discontinuous lower canopy and understory of terra firme rain forest. As these sakis have to leap from tree trunk to tree trunk, they are commonly known as “flying monkeys”. In contrast, saki taxa of the *P. hirsuta* Clade prefer the middle to upper strata of primary rain and seasonally inundated floodplain forests, which strata are interconnected by thick-stemmed vines and hemi-epiphytic climbing shrubs. For that preferred habitat they have adopted a different locomotor pattern, that of horizontal

leaping, and quadrupedal running or hopping across thick horizontal branches and boughs. A significant difference in limb proportions between taxa belonging to each of the two Clades has been measured, with those of the *P. pithecia* Group being longer relative to trunk length (Hershkovitz, 1987a; 1987b). Another important feature in which the *P. hirsuta* Clade distinguishes itself from the *P. monachus* and *P. pithecia* Clades is mean group size and sexual dimorphism. Social groups of taxa belonging to the *P. hirsuta* Clade are larger and multi-male structured, instead of the extended family group that contains only one or sometimes two adult males in taxa belonging to the other Clades. Moreover, contrary to what recent taxonomies



Figure 30. Satellite image taken from the region, where the várzea floodplain of the Rio Solimões borders on that of the Rio Purús. Behind each floodplain are located black-water backwater lakes (rias), such as Lago Coarí, Lago Uauacú, and Lago Ayapuá. A red line indicates where parapatric bald-faced saki *Pithecia hirsuta* is encroaching onto buffy saki *P. albicans* territory. (Below) Portraits of different adult males of Gray's saki *P. hirsuta*. (Above, left) White-masked mutant male *P. hirsuta* that was seen roaming around alone far into *P. albicans* territory north of Lago Uauacú. (Above, right) Adult male buffy saki *P. albicans*; note the black face with the showy albinotic eyebrows and white long-haired hood.

(merely based on museum collections) suggest, we were not able to recognize metachromic sexual dimorphism in any taxon of the *P. hirsuta* Clade. In the field, we failed to distinguish gender among group members of *P. hirsuta*, *P. irrorata*, and *P. albicans*. Nor could we, in captivity, determine their gender without up-close examining the saki monkey's concealed genitals.

Within the Bare-faced Sakis of the *P. hirsuta* Clade we suggest the least eumelanin bleached overall blackish-gray taxon *P. hirsuta* to be the nearest to archetypic taxon. It may well have derived from a founder-colony of proto-*monachus* that once traversed the Rio Juruá in eastern direction. The following pathways of metachromic bleaching and allopatric speciation are recognized. From *P. hirsuta* that occupies the entire interfluvium delineated by the Juruá, Solimões and Madeira Rivers, diverged and radiated away in eastern direction taxon *P. irrorata* after a founder-colony of progressively bleached *P. hirsuta* traversed or circumvented the Rio Madeira (most likely at its upper reaches) during one of the late-Pleistocene glacials. Nowadays, taxon *P. irrorata* occupies the entire interfluvium delineated by the Madeira, Amazonas and Tapajós-Juruena Rivers. Its overall coat is advanced eumelanin bleached in comparison with that of *P. hirsuta*, and albinotic in the distal half of the hood, the hands and feet. Its tail is less bushy, the hairs more curly. *Pithecia irrorata* has an almost bare face, and its forehead is only halfway covered by an albinotic hood that does not conceal the cheeks and temples. As a result, the monkey's profile looks more pronounced. Metachromic skin and fur characters of the head that play such an important role in the taxonomy of monkeys like *Pithecia*, *Sapajus* and *Ateles* are often poorly preserved in museum specimens. Hence, the confusion in most hitherto elaborated taxonomic reviews of these genera. Zoological collections all over the world have lumped misidentified taxa, such as *P. hirsuta* and *P. irrorata*, under the latter. Some leading taxonomists even attribute sexual dimorphism to the Bare-faced Sakis. From *P. hirsuta* to the west diverged taxon *P. vanzolinii*, after a progressively bleached founder-colony of *P. hirsuta* traversed the Rio Envira. *Pithecia vanzolinii* is now confined to the headwaters of the Rio Juruá. It differs in the albinotic lower limbs and ventral parts that contrast much with the blackish-gray dorsal parts and tail.

From *P. hirsuta* to the north derived the overall near-albinotic taxon *P. albicans* that is pheomelanin bleached orangish-yellow only on the lower limbs. Buffy Sakis *P. albicans* occupy the northernmost dead-end distribution of the *P. hirsuta* Clade, which is delineated by the untraversable lower Solimões River in the north, the lower Juruá River in the west, and the lower Purús River in the east. Buffy Sakis are parapatric with the more opportunistic Gray's Sakis *P. hirsuta*, from which they once derived. At its southern limit, its distribution shows an open end running across the Rio Tapauá axis. After it traversed the Rio Tapauá to the north, Gray's Saki *P. hirsuta* was, and still is expanding its range northwards to the cost of the Buffy Saki *P. albicans*. This example may well demonstrate that progressively bleached to albinotic primate taxa that occupy dead-end distributions will eventually go extinct. East of the Rio Coarí and north of the Rio Tapauá - a left-bank tributary of the Rio Purús - we have confirmed the sympatric occurrence of the taxa *P. albicans* and *P. hirsuta*, with *P. hirsuta* advancing onto *P. albicans* as far north as Lago Ayapuá (Fig. 30). North of the Ayapuá contact zone in territory exclusively occupied by *P. albicans*, we once spotted and photographed a solitary young male, its head pelage resembling that of male White-faced Saki *P. pithecia* from the Guianas (Fig. 30). We assume that this male was a progressively bleached deviant color morph of taxon *P. hirsuta* that was expelled from or forced to leave its parental group. It may have ventured into adjacent *P. albicans* territory north of Lago Uauacú. As we have often seen *P. hirsuta* groups opportunistically penetrating far into white-water floodplain forest (várzea), this metachromic deviant near-albinotic, sexually dimorphic mutant male of taxon *P. hirsuta* in theory could become the founding father of a new taxon. This could happen after this young male would have attracted one or a few *P. albicans* females to form a small reproductive family group. It then would have to survive making a year-round living in the extensive várzeas found along the south bank of the Rio Solimões. We have never seen any saki, uakari or other seed-predating monkey occupying that ecological feeding niche in the várzeas that fringe the right bank of the middle Rio Solimões. Perhaps, this hypothetical scenario may also explain how metachromic sexual dimorphism in primates could have evolved.

In figure 31, we have visualized the distributions, allopatric speciation, radiation and supposedly followed pathways of metachromic bleaching in all known Woolly Monkeys, genus *Lagothrix*. Woolly monkeys are exclusive matrix terra firme rainforest dwellers that under normal circumstances will never enter white-water floodplain forest (várzea). For that reason alone, the distribution of *Lagothrix* is greatly determined by riverine barriers. Within the genus only one monophyletic Clade is recognized. We consider the saturated eumelanin, metachromic least bleached Poeppig's Woolly Monkey taxon *La. poeppigii* with its overall black to dark chestnut-brown coat the nearest to archetypic woolly monkey. In the north, *La. poeppigii*'s distribution is confined by the Amazon River, in the east by the Rio Juruá that is also fringed with extensive várzeas, and in the south and west by the

foothills of the Andean Mountain range. From *La. poeppigii* derived in western direction the Peruvian Yellow-tailed Woolly Monkey *La. flavicauda*, which has (disputedly) been upgraded to its own genus *Oreonax*. It occurs in parapatry with *La. poeppigii*, but genetically isolated from it, as it lives in high-altitude Andean cloud forest. With its albinotic lower half of the circumocular rings, facial muzzle, chin and pheomelanin bleached yellow tail the taxon is following a pheomelanin pathway towards albinotic. From a founder-colony of somewhat eumelanin bleached *La. poeppigii* that traversed or circumvented the upper Rio Juruá and then radiated to the east and north, the darkbrown to black headed taxon *La. tschudii* derived. Its coat is overall dark gray-brown colored, becoming blackish on all five limbs. It occupies the entire interfluvial delineated by the Juruá, Solimões-

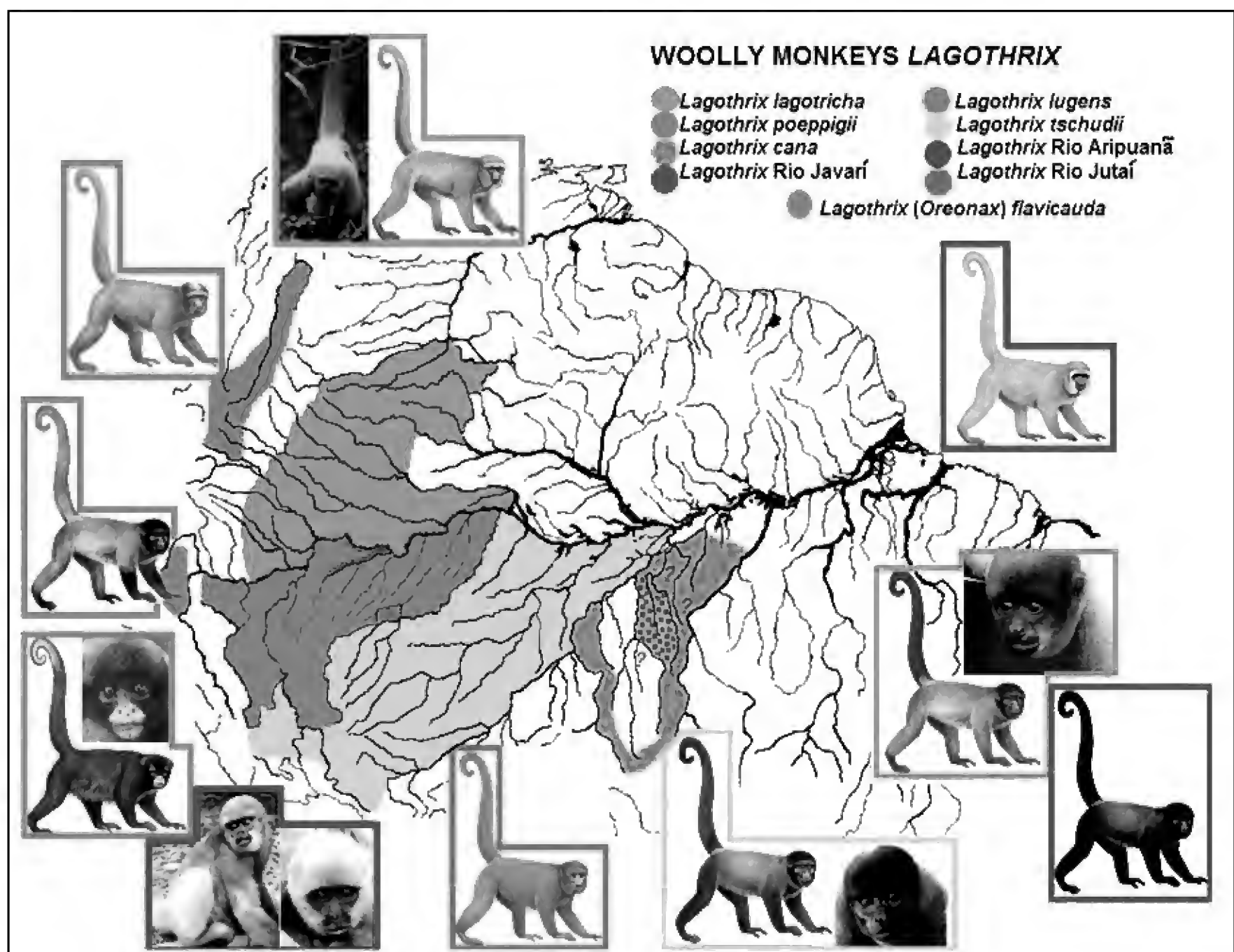


Figure 31. Distributions, allopatric speciation, radiation, and supposed eumelanin pathways of metachromic bleaching in all known Woolly Monkeys genus *Lagothrix*.



Amazonas and Madeira Rivers. From *La. tschudii* in eastern direction diverged the Black-headed or Geoffroy's Gray Woolly Monkey taxon *La. cana*, its entire coat progressively eumelanin bleached, light-gray colored, with a dark-gray to black head. Only as recent as the late-Pleistocene or early Holocene, an advanced eumelanin bleached founder-colony of *La. tschudii* must have traversed or circumvented the upper Madeira River north of the Rio Jí-Paraná (also known as Rio Machado) in eastern direction. It then extended its range by passing the geographic barrier formed by the extensive Tenharim Savanna in Rondonia alongside its southern border. This way, it could enter the interfluvium delineated by the Madeira, Amazonas and Tapajós Rivers. Circumventing the extensive Tenharim Savanna, taxon *La. cana* apparently missed the narrow entrance to the north that exists between the upper Rio Jí-Paraná and the Rio Roosevelt. This could well explain why woolly monkeys are absent from the entire Rios Madeira/Aripuanã interfluvium north of the Rio Marmelos. The relatively recent occupation by *La. cana* of the entire interfluvium delineated by the Madeira, Aripuanã, Amazonas and Tapajós Rivers is near to its completion. Taxon *La. cana*'s current northernmost distribution gets to a halt at the latitude running across the upper reaches of the *Abacaxis* and Andirá Rivers, not much south of the untraversable Rio Amazonas. We assume that only when *La. cana* invaded all smaller interfluviums east of the Rio Aripuanã and west of the Rio Tapajós, it began to displace the All-black Woolly Monkey that in the far geological past evolved in the area east of the (proto)-Madeira River. This newly identified woolly monkey still has to be collected and described. We here provisionally allocate the common name "Rio Aripuanã Black Woolly Monkey" to this fully saturated eumelanin, all-black taxon. Apparently, as it occupies the same ecological niche as newcomer *La. cana*, the Rio Aripuanã Black Woolly Monkey finds itself on the verge of extinction. It is smaller, lives in small, socially less complex family groups, and its coat is in metachromic respect the most primitive or archetypic. It lives in sympatry with *La. cana*, but only hangs on in a small enclave distribution situated between the lower to middle Rio Aripuanã and the Rio Acarí. It may well represent the ancient, most original, archetypic taxon of all Woolly Monkeys genus *Lago-*

*thrix* that evolved in the Late-Pliocene east of the proto-Madeira River, fully isolated from the rest of the Amazon.

Woolly monkeys also radiated into the northwestern Amazon, most likely after a founder-colony of taxon *La. poeppigii* circumvented or traversed the upper Amazon River in Peru (where it is called Río Marañón). Two progressively eumelanin bleached forms that derived from *La. poeppigii* once must have occupied the Colombian Amazon: the euchromic light-gray Colombian Woolly Monkey taxon *La. lugens* that occurs at high altitudes in the foothills of the South-Colombian Andes and in the upper Río Magdalena valley, and the Brown or Humboldt's Woolly Monkey taxon *La. lagotricha*. The coat of taxon *La. lugens* is eumelanin bleached charcoal to light-gray colored, but lacks any mixture with brown. On the head, a mid-dorsal stripe and a rim across the eyebrows are advanced bleached to euchromic. Mean body size and weight in *La. lugens* are the largest among all extant woolly monkeys. *Lagotricha*'s coat is progressively eumelanin bleached light-brown colored, except for the blackish hands and feet. Its head is light-brown colored, with a slightly bleached yellowish eyebrow rim and sideburns aside of the blackish-brown face. Taxon *La. lagotricha* ranges across the Colombian, Venezuelan and NW Brazilian Amazon.

Most interestingly, we confirmed the small distribution of a newly identified, advanced pheomelanin bleached, overall orange-colored taxon in the upper reaches of the Rio Jutáí. A founder-colony of advanced pheomelanin bleached *La. poeppigii* mutants pushed out of *La. poeppigii* territory must once have successfully adapted to white-water seasonally inundated floodplain forest (várzea) located between the east bank of the upper Rio Jutáí and the west bank of the Rio Juruá, near the town of Eirunepé. We were not able to determine the exact range of the Rio Jutáí Woolly Monkey, for the area is inhabited by uncontacted Amerindians of the Korubo tribe (so-called "caçeteiros") that are known to kill any non-indigenous intruder.

We encountered in the zoological collection of the Brazilian Museu Goeldi (MPEG, Belém-PA) an overall orange-colored stuffed juvenile specimen that was deposited without collecting data. This very animal is depicted in Da Cruz Lima's 1945 Mammals of Amazônia. We here provisionally name it the "Rio Jutáí Orange Woolly Monkey".



In addition, we found an albinotic overall cream-colored taxon that we provisionally named the “Rio Javari Fair Woolly Monkey” *Lagothrix* sp. It resembles much Humboldt’s Woolly Monkey taxon *La. lagotricha*, but its pelage is longer, softer and silky, besides being overall advanced eumelanic to cream-white colored. It has long-haired white sideburns alongside a pitch-black face, muzzle and chin. A near-albinotic ancestral founder-colony must once have been driven out of *La. poeppigii* territory somewhere near the northernmost border of its distribution. This colony must have been forced to make a living in the white-water floodplain forests (várzeas) that stretch out along the south bank of the Rio Solimões (near the town of Tabatinga) all the way to the left-bank várzeas of the lower Rio Javari. Under normal circumstances this type of habitat should be consid-

ered inappropriate for woolly monkeys to guarantee a durable and sustainable living. This seems to be another case where a progressively bleached, near-albinotic founder-colony of *La. poeppigii* has been driven into a (for woolly monkeys) marginal habitat - seasonally white-water inundated floodplain forest (várzea). According to our theory of allopatric primate speciation, albinotic fair woolly monkeys must have diverged this way from archetypic, saturated eumelanin, dark brown coated *La. poeppigii*. Apparently, it has survived until today in geographic sympatry, but ecological parapatry (inhabiting adjacent but different habitats) with taxon *La. poeppigii*, the species it derived from. In 2002, the second author, while at Colombia University, NY, ran the mtDNA sequences of the Rio Javari Fair Woolly Monkey using earlier preserved DNA-samples. He found 4% divergence from sympatric

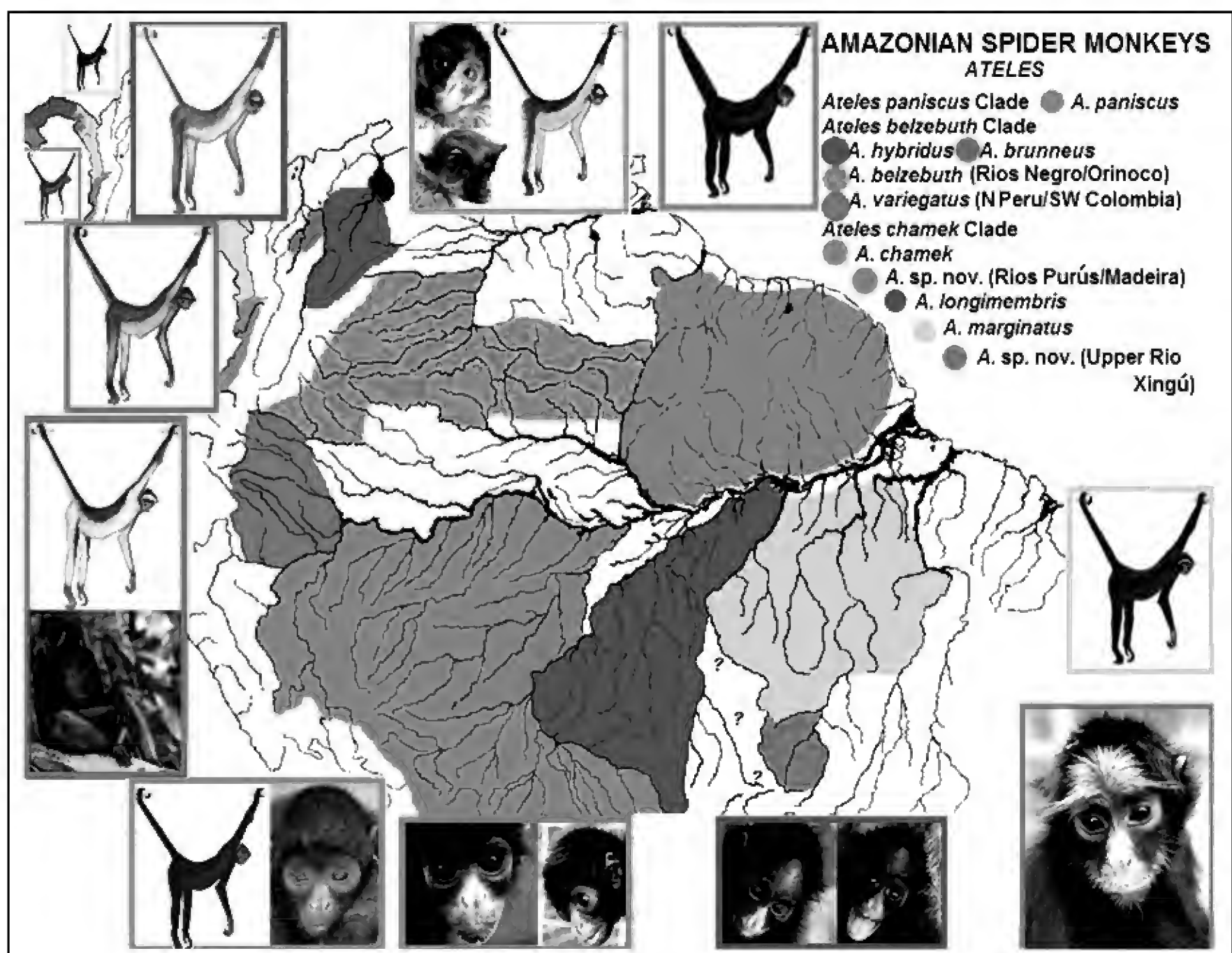


Figure 32. Distributions, allopatric speciation, radiation, and supposed pathways of metachromic bleaching followed in all known Spider Monkeys genus *Ateles* that occur in the Amazon and along the Pacific coast of Ecuador and Colombia.

*La. poeppigii* and over 7% from the allopatric taxon *La. lagotricha*. The AMNH holds three well-preserved skins of the Rio Javari Fair Woolly Monkey *Lagotrix* sp., which were collected by the Olalla Brothers in 1927 along the south bank of the Rio Solimões, somewhat upstream from the town of Tabatinga. All three specimens are misidentified as *La. lagotricha* (Humboldt, 1812).

For Spider Monkeys genus *Ateles*, allopatric speciation, radiation, and phylogeography along different pathways of metachromic bleaching are depicted in figures 32, 33. Four monophyletic cladistic Groups or Clades are recognized: *A. paniscus*, *A. chamek*, *A. belzebuth*, and *A. geoffroyi*. Spider monkeys have evolved during the Pliocene in the Guayanian Shield, most likely from a precursor of the most ancient of the four extant monophyletic cladistic Groups, the *A. paniscus* Clade. The Red-faced Black Spider Monkey *A. paniscus*

from the Guianas represents the nearest to archetypic extant taxon within the genus. This assumption is based on some unique primitive characters that are not seen in other spider monkeys. Here we mention: the presence of a vestigial thumb or, if lacking, at least the metacarpal of the first digit that is maintained in the hand; its incapacity of using the tip of the prehensile tail in picking and manipulating small objects like food items; the overall long-haired coat, in particular around the base of the tail and in the forward directed hairtuft on the forehead that resembles a cap; the overall saturated eumelanin black coat without any sign of early eumelanin bleaching; the advanced pheomelanin bleached bright-red bare face lacking whiskers; the frequent occurrence of albinotic blue-colored eyes; the albinotic cream-white colored, hypertrophied, pendulous clitoris in females and cream-white protruded anus in both sexes, whereas

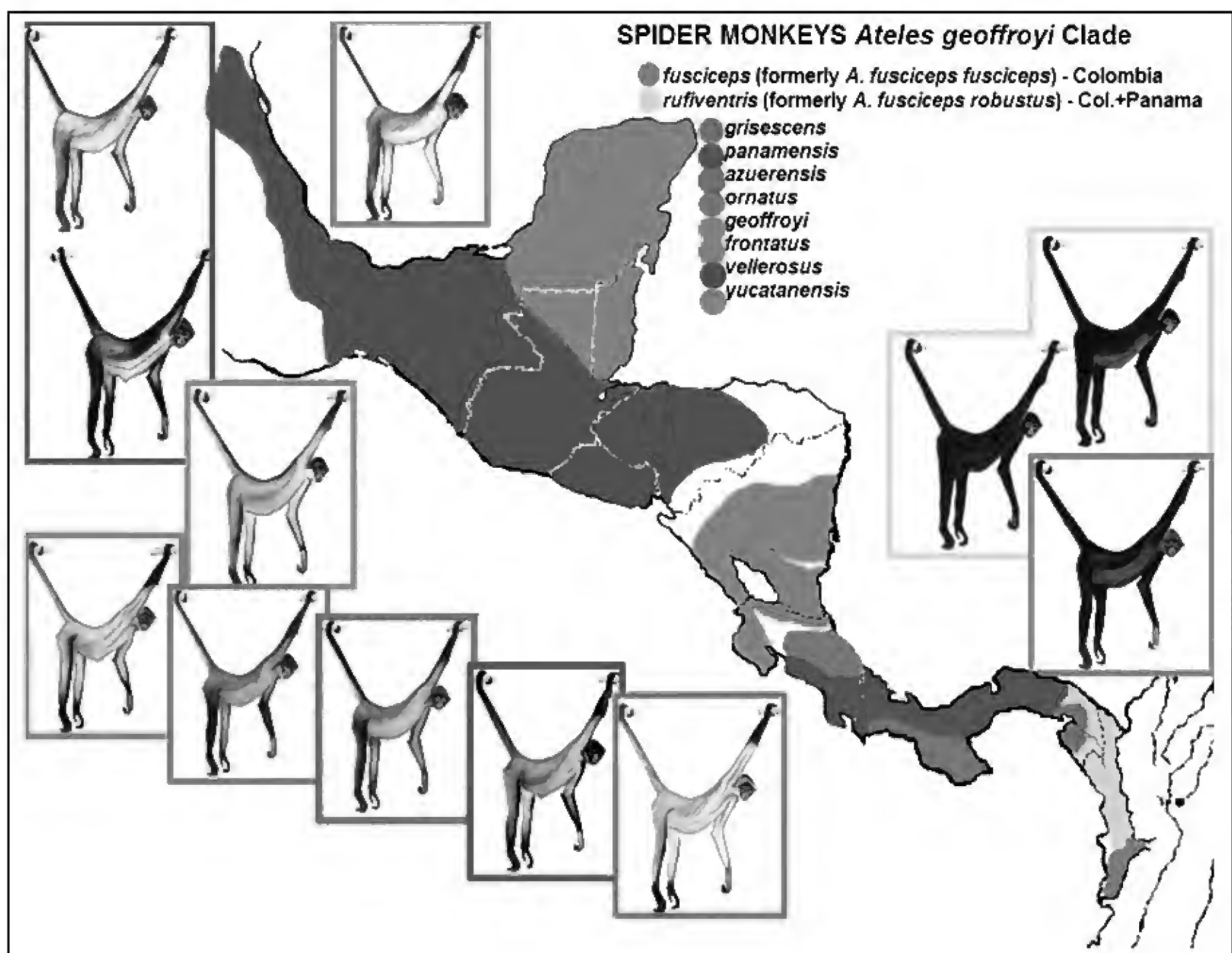


Figure 33. Phylogeographic distribution, allopatric speciation, radiation and metachromic diversification in all known Spider Monkeys (*Ateles*) that occur from the Pacific coast of W Ecuador and NW Colombia far into C America as far N Mexico.

the clitoris is long, flattened and lacking the musculature to erect during foreplay and copulation (Van Roosmalen, 1985a). Moreover, spider-monkey matriarchal social organization is markedly expressed in (leading) female's body size, which in *A. paniscus* may exceed that of males; and in the permanent fusion-fission social structure centered around alpha-females that lead foraging parties on day ranges. As such, complete gatherings of all twenty or so members of a social grouping will never happen (Van Roosmalen, 1985a). This specific type of social organization that is unique among Neotropical primates may well be related to the specific phytosociological composition, phenology and physiognomy of the more ancient, more heterogeneous type of primary terra firme rain forest that evolved uniquely and without major interruptions during the last 60–70 million years on the Guayanan as well as on the Brazilian Shield. Here, available food sources are generally widely dispersed, and rarely clumped at any time of the year. Maturation of nutritious large-seeded fruits - *A. paniscus* is a mature-fruit specialist frugivore - is slower and species-specifically stretched out over longer periods of time (Van Roosmalen, 1985b). Mast-fruiting, as commonly seen in tropical rainforests on other continents, is a phenomenon that does not exist in this ecosystem. Hence, the early evolution of semi-brachiation (brachiation with the help of a prehensile tail) as the principal locomotor pattern, and the fusion-fission type of social structure during traveling and foraging took place in ancestral spider monkeys as the principal adaptation of a large-bodied monkey to a well-defined ecological feeding niche, in a biome that took over 60 million years to develop. It may well explain why the *A. paniscus* Clade did not speciate and radiate any further, as the distribution of extant *A. paniscus* is still confined to the larger part of the Guayanan Shield.

Most plausibly somewhere in the late-Pliocene, from an agouti or saturated eumelanin all-black ancestor of *A. paniscus* derived the phylogenetically distantly related, nearest to archetypic Black Spider Monkey taxon *chamek* of the *A. chamek* Clade. It is distributed south of the Amazon as far south as the Brazilian Shield (in Rondonia and Mato Grosso states). North of the Amazon, the Brown Spider Monkey taxon *A. brunneus* that ranges in N Colombia (in an area confined by the Sierra Nevada

Mountains), may represent the least eumelanin bleached, nearest to archetypic taxon of the *A. belzebuth* Clade. Moreover, in the Pacific coastal forests of Ecuador and Colombia is found the saturated eumelanin Brown-headed Spider Monkey taxon *A. fusciceps* (formerly *A. fusciceps fusciceps*). Along the Pacific coast of N Colombia and S Panama is found the all-black but dark red-bellied Colombian Black Spider Monkey taxon *A. rufiventris* (formerly *A. fusciceps robustus*). All-black Brown-headed Spider Monkey taxon *A. fusciceps* may therefore represent the nearest to archetypic taxon of the *A. geoffroyi* Clade (Fig. 32).

Within the *A. chamek* Clade, nominate *A. chamek* represents the nearest to archetypic taxon. It is saturated eumelanin in its overall black coat color and blackish or slightly bleached pinkish circumocular rings and/or facial muzzle, and in the forward directed black hairtuft on the forehead. It ranges across a large part of the Amazon basin delineated by the Amazon River in the north, the Andes Mountains in the west, the highlands of the Brazilian Shield in the south, and the Purús and Guaporé Rivers in the east. Like the other taxa of the *A. chamek* Clade, the Black-faced Black Spider Monkey *A. chamek* is only found in patches of terra firme rain forest close to major waterbodies, such as lakes, rivers, and creeks. It frequents in particular seasonally inundated marsh forest and black- and clear-water floodplain forest called igapó. We have never spotted spider monkeys belonging to the *A. chamek* Clade in matrix primary rainforest of the hinterland at distances of over ten km from any major waterbody. There, spider monkeys of the *A. chamek* Clade are commonly replaced by woolly monkeys (*Lagothrix*) that occupy the same feeding niche in primary terra firme rain forest. All taxa of the *A. chamek* Clade do laterally migrate to the nearest igapó floodplain forest of clear- and black-water rivers during the 2–3 months lasting fruiting season, which coincides with the peak of the flood. From *A. chamek* diverged and radiated away in eastern direction the Rio Purús Black Spider Monkey that we identified to be new to science. This taxon ranges in the interfluvium between the Purús and Madeira Rivers, south of the Rio Ipixuna and north of the Río Tahuamanu in the Bolivian Amazon, a left-bank tributary of the upper Rio Madeira. The Rio Purús Black Spider Monkey *Atheles* sp. is having a near-albinotic cream to pink

colored muzzle, chin, and ears, and a triangular patch of short, backward directed black hairs on the forehead instead of a cap. After a founder-colony of the Rio Purús Black Spider Monkey traversed the Rio Madeira to the east, the Long-limbed Black Spider Monkey *A. longimembris* diverged. This taxon was already identified as a distinct species by Da Cruz Lima (1945) based on two specimens that were collected by Leo E. Miller along the upper Rio Jí-Paraná in Mato Grosso during the first part of the 1914 Roosevelt-Rondon Expedition. It was first described as *Ateles longimembris* by Allen (1914). Holotype and paratype of *A. longimembris* deposited in the zoological collection of the AMNH under No. 36909 were later misidentified as *A. chamek* and therefore not included in Kellogg & Goldman's (1944) revision of the Spider Monkeys genus *Ateles*. The Latin name that Allen (1914) attributed to this taxon relates to the "*excessively long tail and limbs, the tail length very nearly twice the length of head and body*". Aside of its elongated and slender limbs, taxon *A. longimembris* is further characterized by the pitch-black face and ears, except for a pale cream-white albinotic triangular patch on the nose, and a wide triangular patch on the forehead that is barely covered with sparse backward directed, stiff, black hairs. Another character of this taxon is the relatively robust incisors and canines that look oversized so that the lips seem unable to conceal them. This feature gives adult Long-limbed Black Spider Monkeys taxon *A. longimembris* a bulldog-like appearance. Moreover, its loud or long-distance calls that are so typical for other spider monkeys do not carry far. They sound like bird whistles blowing in the wind. The distribution of *A. longimembris* is confined by the Rio Madeira in the west, the lower Amazon River in the north, the Rio Tapajós-Juruena in the east and the Rio Jí-Paraná in the south. From a founder-colony of *A. longimembris* that once traversed the Rio Tapajós-Juruena to the east derived the White-whiskered Black Spider Monkey *A. marginatus*. It is all-black and only euchromic in the small triangular forehead patch or blaze formed by backwards directed white hairs. However, we have seen also adult free-ranging *A. marginatus* that had black forehead patches. This taxon occupies the interfluvium delineated by the Rios Tapajós and Teles-Pires in the west, the lower Amazon River in the north, the Rios Tocantins and Araguaia in the east, and the upper Rio Teles-Pires

or Rio Minisuiá-Miçú (both right-bank tributaries of the upper Rio Tapajós) in the south. After a somewhat eumelanin bleached founder-colony of *A. marginatus* once traversed the upper Rio Teles-Pires south of the *A. marginatus* distribution, a new taxon diverged that we name the Upper Rio Xingú White-whiskered Brown Spider Monkey. Its coat is chestnut-brown dorsally, and lighter brown on the ventral parts. The snow-white semi-crescent blaze is much larger than in *A. marginatus*. It widens above the eyes into long sideways directed streaks. This newly identified taxon distinguishes itself also from taxon *A. marginatus* in the long white whiskers that run from below the eyes across the lips and chin. Moreover, facial skin is pink to flesh-colored in the circumocular rings, muzzle, lips and chin. Within the monophyletic *A. chamek* Clade the White-whiskered Brown Spider Monkey from the Upper Rio Xingú represents the furthestmost eumelanin bleached taxon that, in accordance with our theory, metachromically and phylogeographically radiated farthest away from archetypic Black-faced Black Spider Monkey taxon *A. chamek*.

Within the *A. belzebuth* Clade, we recognize the dorsally saturated eumelanin darkbrown Brown Spider Monkey taxon *A. brunneus* as the nearest to archetypic taxon. Belly and inner limbs are eumelanin bleached light-brown colored. The triangular forehead patch formed by backward directed hairs is only slightly bleached brownish-black colored. Taxon *A. brunneus* is found in N Colombia, between the Cauca and Magdalena Rivers. It is taxonomically treated as a subspecies of *A. hybridus*. In the far geological past, the *A. belzebuth* Clade could well have derived from the archetypic, saturated eumelanin, all-black taxon (*A. geoffroyi*) *A. fusciceps* (formerly *A. fusciceps fusciceps*) of the *A. geoffroyi* Clade that occurs west of the Andes Mountains in the Pacific coastal forests of Ecuador and Colombia. An ancestral founder-colony of *A. fusciceps* once may have circumvented the Sierra Nevada north of it and diverged into ancestral *A. brunneus* in the western part of the lower Río Magdalena valley. After a progressively eumelanin bleached founder-colony of *A. brunneus* traversed the Río Magdalena to the east, the light-brown and silvery-white colored Variegated Spider Monkey taxon *A. hybridus* could have derived. It ranges from the northern Colombian Río Magdalena Basin into the southwesternmost corner of Venezuela, in



the foothills of the Sierra Nevada mountain range (near the city of Mérida). Inner parts of limbs, belly and the small triangular forehead patch are silvery white in taxon *A. hybridus*, whereas the rest of the coat is light-brown colored. An advanced eumelanin bleached founder-colony of *A. hybridus* once may have circumvented the Sierra Nevada Mountains to the east and reached the headwaters of some of the Río Orinoco's tributaries in Venezuela's Amazonas state. It then diverged into the furthestmost pheomelanin bleached White-bellied Spider Monkey taxon *A. belzebuth*. It ranges from north of the Rio Negro and west of the Rio Branco into the Venezuelan State of Amazonas west of the Río Orinoco, and also far into the lowland Amazon of Colombia. Upper parts, head and dorsal coat of White-bellied Spider Monkeys taxon *A. belzebuth* are light-brown, but their pelage on ventral parts and inner sides of limbs are silvery white, often pheomelanin bleached yellow to orange-colored. The skin of muzzle and chin is pale brown to pinkish colored. The triangular forehead patch or blaze is light brown, and the eyebrows, whiskers, and throat are silvery. From a founder-colony of *A. belzebuth* that once traversed the upper Río Caquetá derived in southwestern direction the southernmost distributed taxon of the *A. belzebuth* Clade, *A. variegatus*. This taxon occurs in the N Peruvian, SW Colombian and eastern part of the Ecuadorian Amazon, east of the Andes Mountains and north of the Amazon River (where the river is called Río Marañón). Its coat is dorsally eumelanin blackish to dark gray, and ventrally euchromic to albinotic silvery-white, except for the dark grayish hands and feet. The legs are silvery white, as are the whiskers and the large blaze or triangular patch on the forehead. Advanced pheomelanin bleached color traits (yellow and orange) as seen in *A. belzebuth* are lacking in *A. variegatus*. In accordance with our theory and the principle of metachromic bleaching, within the belzebuth Clade the most euchromic taxon, *A. variegatus*, has phylogeographically radiated the farthest away from the dark-brownish colored, nearest to archetypic taxon *A. brunneus* (Fig. 32).

Within the *A. geoffroyi* Clade (Fig. 33), we recognize the saturated eumelanin Colombian Black Spider Monkey taxon *A. (fusciceps) rufiventris* (formerly *A. fusciceps robustus*) from the Pacific coastal forests of Colombia and South Panama west

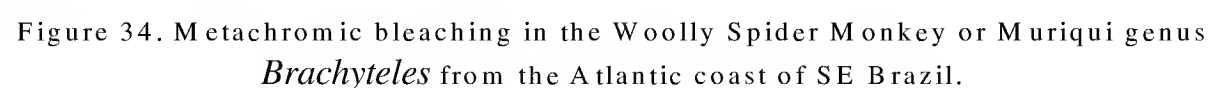
of the Andes Mountains as the nearest to archetypic taxon of the *A. geoffroyi* Clade. Its coat is glossy pitch-black, whereas color morphs of this taxon show a saturated pheomelanin dark red colored belly and genital area. Fur on the forehead is slightly brownish tinged. From taxon *A. rufiventris* derived in southern direction the Brown-headed Black Spider Monkey, the nominate taxon *A. (fusciceps) fusciceps* from the Pacific coastal forests of Ecuador and Colombia. It is slightly eumelanin bleached blackish-gray on the belly, brownish black above, with a yellow-brown anterior crown, grading from brown to black on the nape. It often has a white mustache and beard. Taxa *A. fusciceps* and *A. rufiventris* stand at the base of the monophyletic Central-America Spider-Monkey *A. geoffroyi* Clade, which radiated away in northwestern direction across the Isthmus of Panama into Central America as far north as Mexico. From the Colombian Black Spider Monkey *A. rufiventris* derived the advanced euchromic, near-albinotic (except for the saturated eumelanin feet, hands, lower arms and distal part of the tail) taxon *A. (geoffroyi) grisescens*. However, the validity of this taxon is doubtful, for it has never been seen in the wild. It is thought to occupy a dead-end distribution along the Pacific coast from the Río Tuyra valley in SE Panama into the Cordillera de Baudó in NW Colombia. To the east, its distribution is confined by territory occupied by the Colombian Black Spider Monkey *A. rufiventris*. From *A. rufiventris* diverged in western direction the advanced pheomelanin bleached Ornate Spider Monkey taxon *A. (geoffroyi) panamensis*. It is argued that the form *A. panamensis* is a junior synonym of *A. ornatus*. Taxon *A. panamensis/ornatus* has a golden brown, dark red to orange colored back, with saturated eumelanin black pelage on the top of the head, outer sides of legs, hands, feet and distal part of the tail. It is distributed throughout Panama (from Chiriquí Province as far as E of the Canal Zone) and C+E Costa Rica. From *A. ornatus* (or *A. panamensis*) derived in southern direction the advanced pheomelanin bleached Azuero Spider Monkey taxon *A. azuereensis*. Its back is grayish-brown, somewhat darker than the underside. Outer surfaces of the limbs are black, the top of the head and neck are (brownish)-black. Its distribution is delineated by the Panamanian Pacific coast in the south and east. From the Ornate Spider Monkey taxon *A. ornatus* derived in



northern direction into Nicaragua the advanced pheomelanin bleached, near-euchromic Geoffroyi's Spider Monkey taxon *A. geoffroyi*. It is silvery to brownish-gray on the back, upper arms, and thighs. Its coat (except for the black head, elbows, knees, upper arms, lower legs, hands and feet) is overall orangish and cream-white colored. Its face is black, often with flesh-colored 'spectacles' around the eyes. From *A. ornatus* radiated away, first in western direction and from coastal Costa Rica northwards into Nicaragua, the advanced pheomelanin bleached Black-browed Spider Monkey taxon *A. frontatus*. With its orange, black and white coat *A. frontatus* is the most colorful taxon of the entire *A. geoffroyi* Clade. From taxon *A. frontatus* derived the overall most euchromic bleached Mexican Spider Monkey taxon *A. vellerosus*. Its dorsal surfaces range from black to light brown, and contrast strongly with its lighter abdomen and inner limbs. Flesh-colored skin is often present around the eyes. It occupies the entire northwestern part of the Isthmus containing El Salvador, Honduras (along the N coast into the lowlands of La Mosquitia), Guatemala (including the highlands) and E & SE Mexico. From taxon *A. vellerosus* to the north derived the near-albinotic Yucatán Spider Monkey taxon *A. yucatanensis*. It is characterized by the overall advanced eumelanin bleached, light brown and white colored coat. Its fur is brownish-black on the head, neck, and shoulders, grading into lighter brown on the lower back and hips and contrasting with its silvery-white underside, inner limbs, and sideburns. *Ateles (geoffroyi) yucatanensis* occupies a large distribution containing NE Guatemala, all of Belize, and SE Mexico (Yucatán Peninsula). The near-albinotic taxa *A. vellerosus* and *A. yucatanensis* that occupy dead-end distributions confined by untraversable geographic barriers in the northernmost range of the *A. geoffroyi* Clade, phenotypically do resemble taxon *A. grisescens* (from SW Panama) that occupies the southernmost distribution of the *A. geoffroyi* Clade within the Isthmus. These taxa are equally confined to phylogeographic dead-end distributions, therefore fully concurring with our theory that pretends to unveil and retrace allopatric primate speciation and radiation along phylogeographic pathways of meta-chromic bleaching.

Woolly Spider Monkeys or Muriquis genus *Brachyteles* (family Atelidae) from SE Brazil are

disputedly the largest among New World monkeys (adults weighing up to 11–12 kg). It is estimated that alouattines (howling monkeys) and atelines (woolly, spider, and woolly spider monkeys) split about 16 MYA and that the ancestor of Muriquis (*Brachyteles*) and Woolly Monkeys (*Lagothrix*) separated about 10 MYA from the lineage that would eventually lead to the Spider Monkeys (*Ateles*). Amazonian *Lagothrix* and Atlantic Forest *Brachyteles* are therefore considered to be sister groups (Mittermeier et al., 2013). Two species of Muriquis are recognized: the Northern Muriqui *B. hypoxanthus*, and the Southern Muriqui *B. arachnoides* (Fig. 34). Taxon *arachnoides* is distributed in SE Brazil, through the coastal Serra do Mar in the states of Rio de Janeiro, São Paulo, and (the NE of) Paraná. Its northern limits are the Serra da Mantiqueira and the Rios Paraíba and Paraíba do Sul. Taxon *B. hypoxanthus* historically ranged through the Atlantic Forest in the states of Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro, excluding only lowland forests in the extreme S of Bahia and N Espírito Santo. The northern limit of its distribution was probably the Rio Jequiriçá or the right bank of the Rio Paraguaçu, whereas the southern limit most likely was the Serra da Mantiqueira, in S Minas Gerais state. There, it meets the distribution of the Southern Muriqui taxon *B. arachnoides*. Sexual dimorphism is absent in Muriquis. The Southern Muriqui has a predominantly beige, with light, or dark brown or light gray-brown colored coat. It retains the black pigmentation of the face, palms, and soles of the feet from infancy into adulthood. Adults of both sexes develop only minor depigmentation in small pink or white spots in the pubic region and sometimes on the face. The Northern Muriqui taxon *B. hypoxanthus* has a uniformly beige colored pelage, with light or dark brown or light gray-brown coloration. At birth, the face is black, but at sexual maturity face and genitals lose their pigmentation and become spotty pink or flesh-colored (Fig. 34). Northern Muriquis have a vestigial thumb, which character differentiates them from Southern Muriquis that lack the thumb. The Southern Muriqui seems to be nearer to archetypic woolly spider monkeys than the Northern Muriqui, for the latter is overall progressively pheomelanin bleached near-albinotic in the head characters (white eyebrows, sideburns, and beard), and also in the advanced de-



For Amazonian Howling Monkeys, genus *Alouatta*, allopatric speciation, radiation, and phylogeography along eumelanin and pheomelanin pathways of metachromic bleaching are depicted in figures 35, 36). Two monophyletic cladistic Groups or Clades are recognized: *Al. belzebul* and *Al. seniculus* (Mittermeier et al., 2013). Within the *Al. belzebul* Clade, distributed south of the Amazon, saturated eumelanin all-black howling monkeys of the Amazon Black Howler taxon *Al. nigerrima* range between the Tapajós and Madeira Rivers. A

founder-pair or colony of somewhat bleached *Al. nigerrima* howlers once must have traversed the lower Rio Madeira, most likely lifting on floating logs or on drifting islands covered with chavascal (low type of várzea) forest. Presently, this howler also inhabits almost the entire interfluvium delineated by the Rios Amazonas, Purús and Ipixuna, an area that was formerly occupied by the advanced pheo-melanin bleached yellowish-orange colored Purus Red Howler taxon *Al. puruensis* (belonging to the *Al. seniculus* Clade). We have spotted *Al. nigerrima* howlers in the várzea near Carreiro (opposite the city of Manaus) and, also, as far south as the Rios

Igapó-Açú and Tupana - black-water rivers that empty out into the Rio Madeirinha (a white-water left-bank tributary of the Rio Madeira). It seems that the overall orange-colored resident howler *Al. puruensis* and the all-black invasive *Al. nigerrima* howler do co-exist locally. However, the two taxa do not mix nor interbreed. While conducting a canoe survey during the peak of the flood season in the vast igapó floodplain along the Rio Igapó-Açú and Igarapé Cujubim, we have heard and seen the two taxa belonging to different Clades (*Al. belzebul* and *Al. seniculus*, respectively) in the same general area. The more frugivorous *Al. nigerrima* howler was only seen in the middle of seasonally flooded igapó forest during the peak of fruiting, whereas the more folivorous *puruensis* howler stayed back in the adjacent primary terra firme rain forest. We assume that *Al. puruensis* does so by lack of its

elsewhere preferred habitat - seasonally white-water inundated floodplain forest (várzea). It therefore seems that monkey taxa belonging to different monophyletic clades locally can co-exist, but only if they occupy different feeding niches, and within the local landscape parapatric or partly overlapping habitats. As these two howler taxa are considered valid species, they seem to have sufficiently diverged from one another to impede interbreeding in the contact or overlap zone.

Representing the nearest to archetypic taxon of the *Al. belzebul* Clade, the range of the Amazon Black Howler taxon *Al. nigerrima* may well be considered the center of the Clade's dispersion. From here, the other taxa diverged in eastern direction. From *Al. nigerrima* derived east of the Rio Tapajós the pheomelanin bleached Spix's Howler *Al. discolor*. It has an overall dark-brown to mahogany-

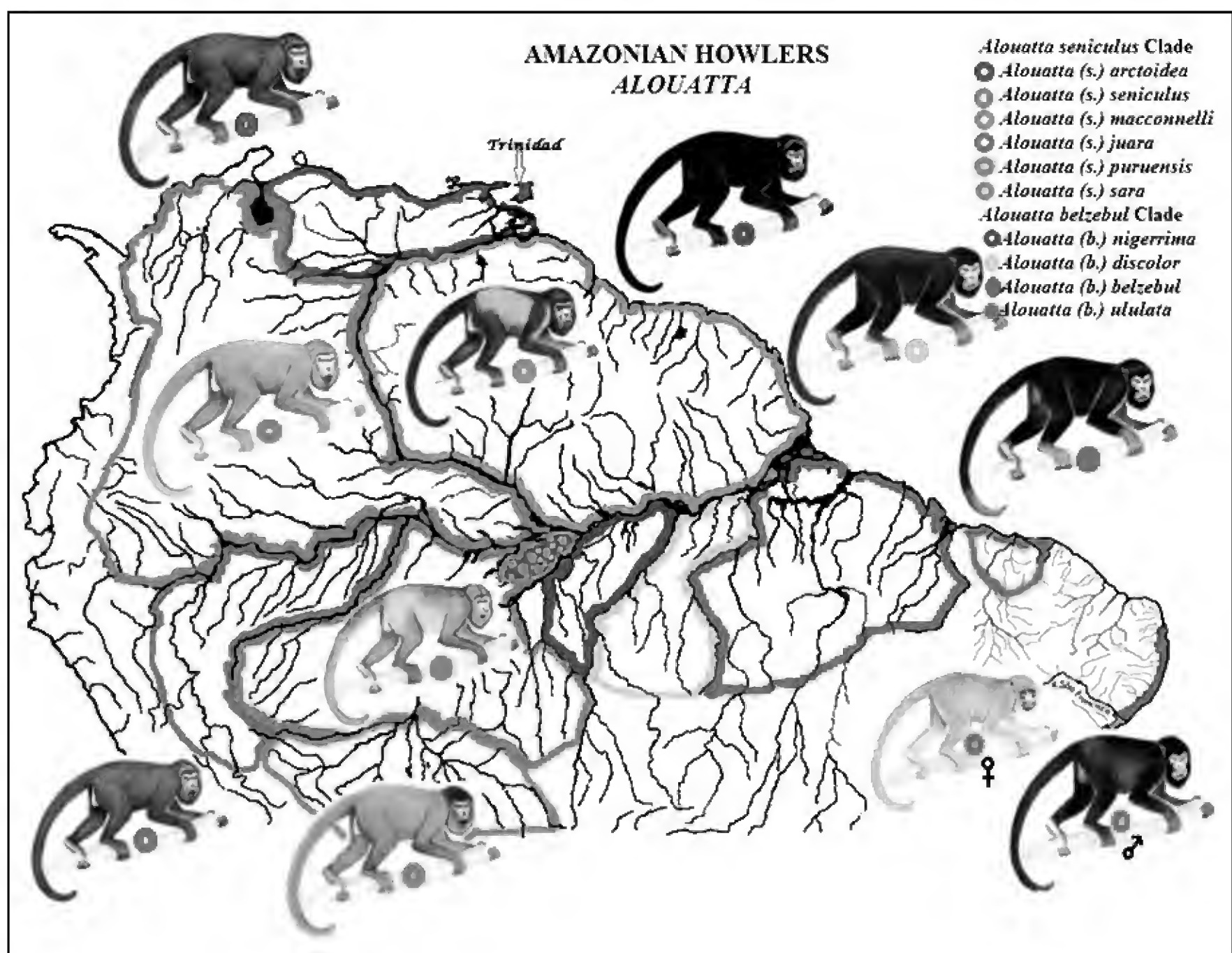


Figure 35. Distributions, allopatric speciation, radiation, and phylogeography along different pathways of metachromic bleaching depicted for all known Amazonian Howlers genus *Alouatta*.

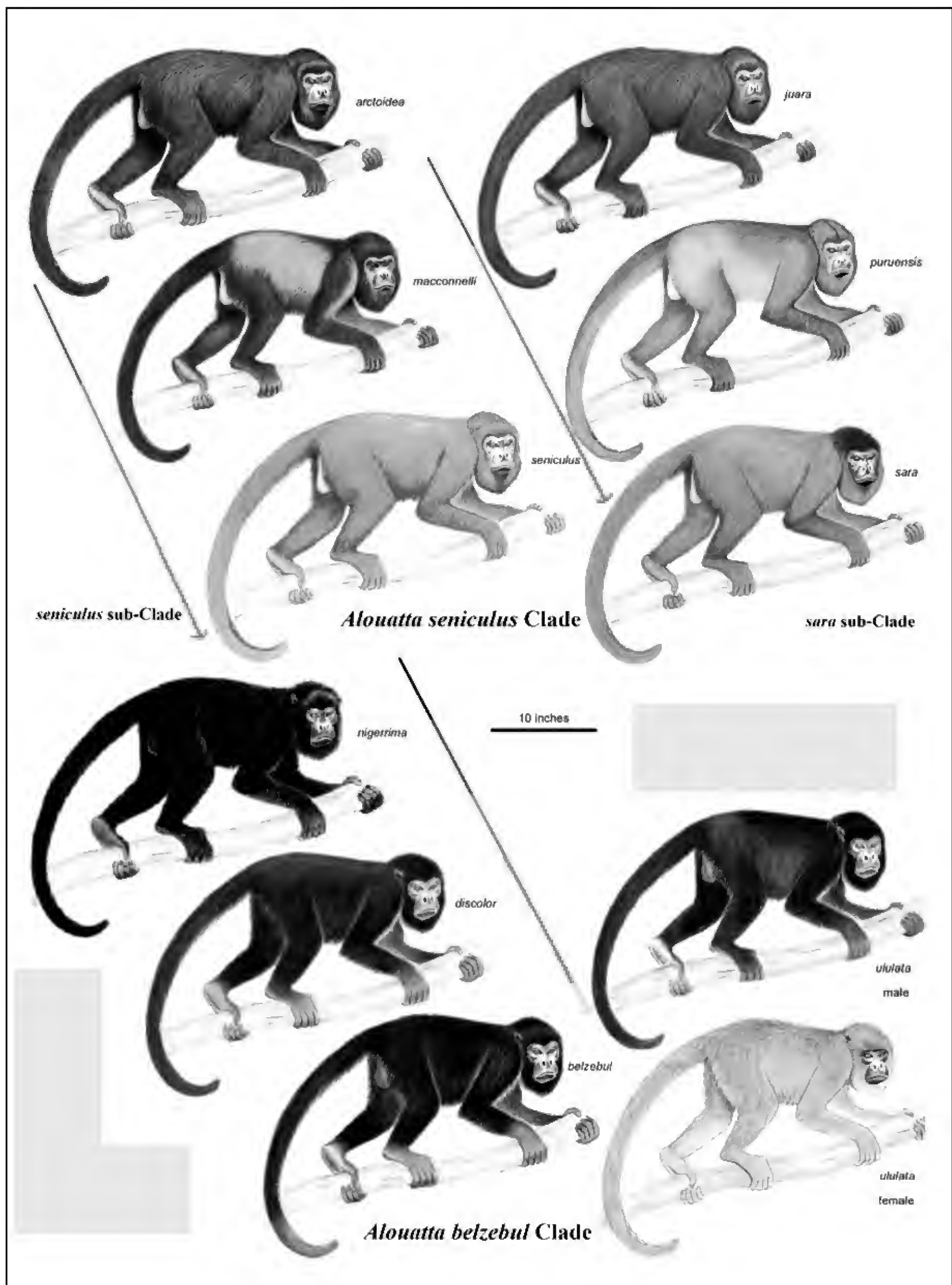


Figure 36. Metachromic variation, radiation, and phylogeography along eumelanin and pheomelanin pathways of metachromic bleaching depicted for all known Amazonian Howlers of the *Alouatta seniculus* and *Al. belzebul* Clades.





Figure 37. Adult male Guianan Red Howler *Alouatta macconnelli*. It was photographed while pulling off a juvenile that tried to seek protection from the human intruder, somewhere along the black-water Rio Jauaperí, a north-bank tributary of the Rio Negro (Courtesy of David Lemmon).

red coat and a rufous-chestnut dorsal band, hands, feet, and tip of the tail. A further pheomelanin bleached founder-colony of *Al. discolor* must once have traversed its eastern distributional limit - the Rio Xingú, Irirí, or Santa Helena (left-bank tributary of the Rio Teles-Pires in Mato Grosso). From Spix's Howler *Al. discolor* derived the dark brown colored Red-handed Howler *Al. belzebul*. This species is progressively pheomelanin bleached in the reddish-brown to yellow hands, feet, tail tip, forehead and back. It is distributed south of the Amazon, east of the Rio Xingú-Irirí, in the states of Pará (including Mexiana, Caviana, and Marajó Islands in the Amazon estuary), Maranhão, Tocantins, and Mato Grosso. West of the Atlantic coast of NE Brazil in the states of Rio Grande do Norte, Paraíba, Pernambuco, and Alagoas, are found enclave populations isolated from what is thought the taxon's former distribution, which must have been continuous through the states of Ceará and Piauí to the Amazonian population. From the Red-handed Howler *Al. belzebul* derived the advanced pheomelanin bleached Maranhão Red-handed Howler *Al. ululata*. This species distributed in NE Brazil occurs in remnant forest patches of dry

forest scrub called caatinga. It enters also the coastal mangrove forests of northern Maranhão, Piauí, and Ceará. The Maranhão Red-handed Howler *Al. ululata* radiated farthest away from the archetypic overall black Central Amazon Black Howler *Al. nigerrima*. It is sexually dichromatic. The male is black with rufous to reddish-brown hands, feet, tip of the tail and flanks. The female is yellowish-brown with sparse grayish hairs, giving it an overall olivaceous appearance (Fig. 36).

Within the *Al. seniculus* Clade we consider the overall dark reddish-brown Ursine Red Howler arctoidea from N Venezuela east of Lake Maracaibo, and from the coast (including the Islands of Trinidad and Tobago) extending S through the llanos to the Río Orinoco, the nearest to archetypic taxon for the monophyletic *Al. seniculus* sub-Clade, which is distributed north of the Amazon. Both sexes have a coat that is dark reddish-brown on the body, contrasting with a darker brown to blackish head, shoulders, limbs, and proximal part of the tail. Male Ursine Red Howlers often have a blackish beard, limbs and tail. From a founder-colony that once traversed the Orinoco River to the east, has derived the advanced pheomelanin bleached Guianan Red Howler *Al. macconnelli*. This taxon ranges east of the Río Orinoco throughout the Guianas, N Brazil (east of the Rio Negro and north of the Rio Amazonas, including Gurupá Island in the Amazon estuary), and S Venezuela (between the Cassiquiare and Orinoco Rivers). The Guianan Red Howler's coat is uniformly dark rufous-brown, the back is pheomelanin bleached yellowish to golden-brown with a dark dorsal stripe, and arms to elbows and legs to thighs are orangish-red. Distal part of the tail is pale-yellow (Figs. 35, 36).

From a founder-colony of further pheomelanin bleached *Al. macconnelli* that once traversed either the upper Rio Negro in the Colombian Amazon, or the Orinoco River at its headwaters, has derived the overall orange-colored Colombian Red Howler *Al. seniculus*. This taxon is now distributed north of the Amazon across E Ecuador and E Peru (east of the Río Huallaga), Colombia, NW Venezuela, and the Brazilian Amazon inbetween the Rio Solimões and Rio Negro. The Colombian Red Howler *Al. seniculus* is overall golden-toned to coppery-red on the body, contrasting with the maroon head, shoulders, limbs, and proximal part of the tail. Male Colombian Red Howlers are much bigger than fe-



males. Within the monophyletic *Al. seniculus* sub-Clade the bright orange-red Colombian Red Howler *Al. seniculus* is phylogeographically the most advanced pheomelanin bleached taxon. It radiated the farthest away from the nearest to archetypic saturated eumelanin, overall dark brown colored Ursine Red Howler *Al. arctoidea*, as such fully concurring with our theory. With respect to the monophyletic *Al. sara* sub-Clade of the *Al. seniculus* cladistic Group that is largely distributed south of the Amazon, we consider the Juruá Red Howler *Al. juara* the nearest to archetypic, least eumelanin bleached (dark brown) taxon. It ranges in the W Brazilian Amazon south of the Rio Solimões, and in the Rio Juruá Basin, extending west into the Peruvian Amazon. It is not sexually dichromatic. Its coat is generally dark reddish-brown, with the middle of the back lighter orange-rufous colored, and limbs and tail base dark rufous to black. The tail is paler, more golden from middle to tip. From a pheomelanin bleached founder-colony that once traversed the Rio Juruá to the east derived the Purús Red Howler taxon *Al. puruensis*. It is distributed across the entire Rios Juruá/Purús interfluvium as far east as the middle Rio Madeira. From there, it extended its range across the upper Rio Aripuanã as far east as the Rio Teles-Pires, and south as far as the Rio Abunã (which forms Bolivia's northern border). The Purús Red Howler *Al. puruensis* is sexually dichromatic. Males are dark rufous or red-brown with a golden upper dorsum and shoulders, whereas females are golden-orange with distal portions of limbs, tail base, and beard dark rufous. From a progressively pheomelanin bleached founder-colony of the Purús Red Howler that once traversed the Río Abunã, has derived the quite distinct Bolivian Red Howler taxon *sara*. It is distributed across the Bolivian Amazon including the entire Río Beni Basin, and east as far as the Rios Mamoré/Guaporé interfluvium. The Bolivian Red Howler's coat is brick-red above, with limbs, head, and proximal part of the tail darker, more rufous colored. It represents the most advanced pheomelanin bleached taxon of the *Al. sara* sub-Clade (Fig. 36). It occupies a dead-end distribution in the south bordering the drier savanna and Chaco area (Fig. 35). Going further southwards begins the distribution of the Paraguayan Howler *Al. caraya*.

For extra-Amazonian Howling Monkeys genus *Alouatta*, allopatric speciation, radiation, and phylo-

geography along eumelanin and pheomelanin pathways of metachromic bleaching are depicted in figures 38, 39. Four non-Amazonian monophyletic Clades are recognized: the Brazilian Brown Howler *Al. guariba*, the Paraguayan Howler *Al. caraya*, the Central American Mantled Howler *Al. palliata*, and the Mexican Black Howler *Al. pigra* (Mittermeier et al., 2013). The Brown Howler *Al. guariba* Clade consists of two populations that may represent different valid taxa or species: the Northern Brown Howler *Al. guariba* and the Southern Brown Howler *Al. clamitans*. Taxon *Al. guariba* ranges in the Atlantic Forest from the Rio Paraguaçu, Bahia State, along the coast south as far as Rio Paraíba in Rio de Janeiro State. Inland, it extends into Minas Gerais State. The Southern Brown Howler *Al. clamitans* is distributed in the Atlantic Forest south of Rios Doce and Jequitinhonha, south as far as Rio Grande do Sul State. Taxon *Al. guariba* is not sexually dichromatic and both sexes are red-fawn, with females usually somewhat duller in color. Taxon *Al. clamitans* is generally dark reddish-brown, with males often being lighter colored than females. Males from São Paulo are orange-red to red-brown with a red belly, whereas males from Santa Catarina and Rio Grande do Sul are bright red-orange, having dark brown feet. Females are overall dark brown or blackish. The Northern Brown Howler *Al. guariba* is the lesser metachromic bleached. Taxon *Al. clamitans* derived from it, the males progressively following the pathway of pheomelanin bleaching. The further south it ranges, the more the male's overall coat color tends to red-orange or bright orange (Fig. 39).

The Paraguayan Howler *Al. caraya* forms a monotypic Clade. It is a sister species to the Amazonian red howlers of the *Al. seniculus* Clade. It diverged from a common ancestor about 4 MYA. The Paraguayan Howler *Al. caraya* is distributed across C Brazil, south of the states of Pará, Tocantins, Maranhão, and Piauí, west into the Pantanal, south into Paraguay, E and SE Bolivia, and maybe also into NW Uruguay. Much of its range is in the 'cerrado' of central Brazil and semi-arid 'caatinga' forest scrub in NE Brazil, where it uses gallery and riparian forest and patches of seasonal (semi)-deciduous 'cerradão' (a type of savanna forest). Adults of *Al. caraya* are sexually dichromatic, but both sexes are blond at birth. Mature males are generally uniformly black. Females and young of

either sex are pale grayish-yellow to golden-brown. Male Paraguayan Howlers *Al. caraya* from Bahia and Goiás are black, but those from Mato Grosso and Paraná are black with a brown back and hind parts. Males from São Paulo and Minas Gerais States are brown-black, with yellowish hands, feet, belly, and tail tip. In all male individuals the face is invariably dark, the fur is stiff and lengthy, and the beard is prominent. The scrotum is rust-red colored.

The Pacific Coastal and Central American Mantled Howler *Al. palliata* is, based on geographic distribution, divided in five taxa that could well represent distinct valid species: *Al. palliata* from NE Guatemala, ranging east to E Costa Rica or W Panama; *Al. aequatorialis* from the southern distributional limits of *Al. palliata* ranging through

the Darién into W Colombia, W Ecuador, and south as far as NW Peru; *Al. mexicana* ranging from S to SE Mexico and Guatemala following the southernmost distribution of the Central American Black Howler *Al. pigra*; *Al. coibensis* from Coiba and Jicarón Islands in SW Panama; and *Al. trabeata* from the Azuero Peninsula in SW Panama (Fig. 38). The coat of the Mantled Howler is smooth, very short and upright, being silky black with a mantle of longer, gold or yellowish-brown fur along the flanks. Adult males have a white scrotum.

The Central American Black Howler *Al. pigra* is monotypic. It is distributed across SE Mexico, Belize, and N to C Guatemala. Fur of *Al. pigra* is notably long, soft, and dense. Adults are not sexually dichromatic. They are overall black with traces of brown on the shoulders, cheeks, and back. The



Figure 38. Distributions, allopatric speciation, radiation, and pathways of metachromic bleaching followed in all extra-Amazonian Howling Monkeys genus *Alouatta*. Two Clades occur south of the Amazon: *Al. guariba* from the E Brazilian Atlantic forest, and *Al. caraya* from the 'cerrado' and 'cerradão' of the Central Brazilian Plateau. Along the Pacific coast of Ecuador and Colombia, far into Central America, occur the *Al. palliata* and *Al. pigra* Clades.

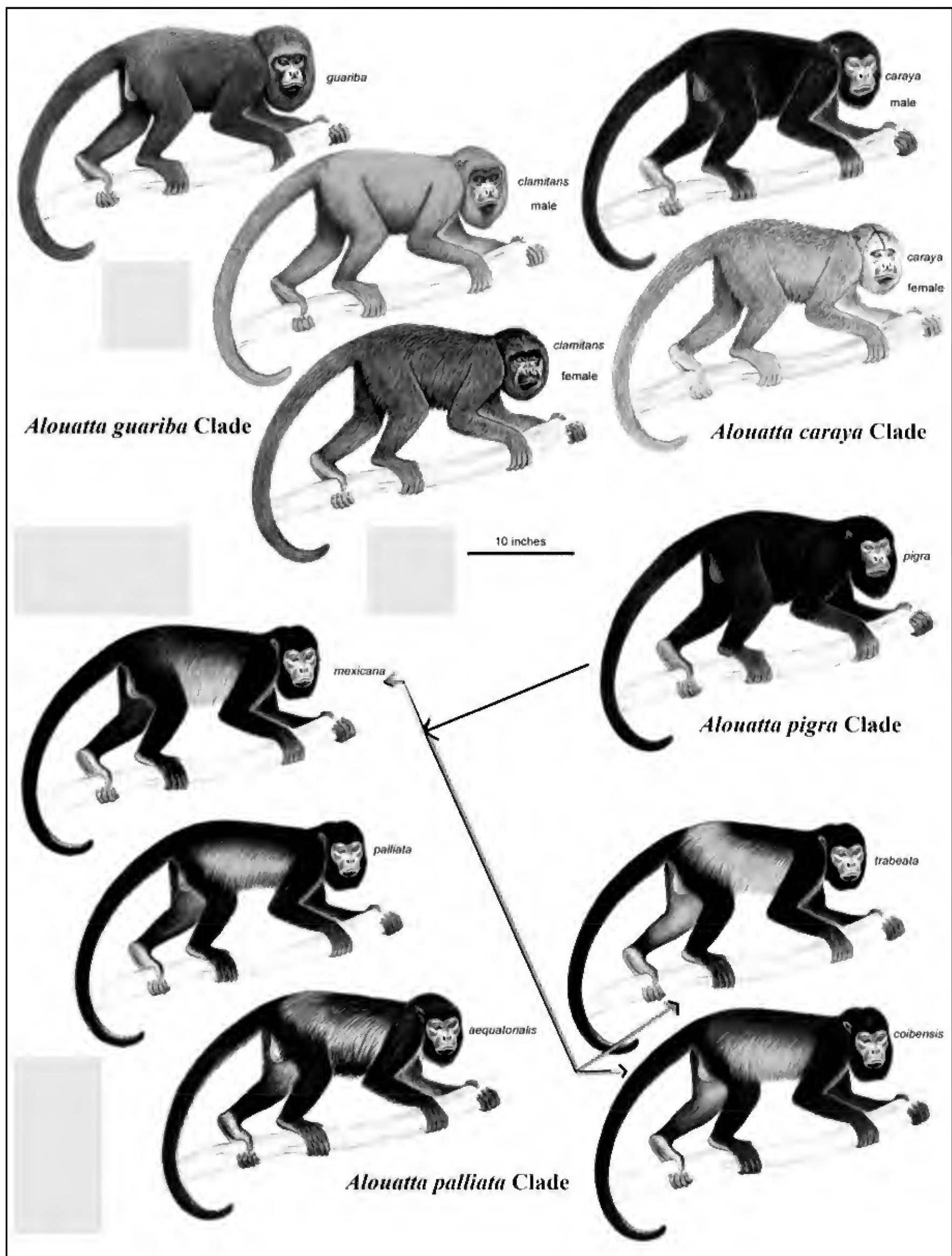


Figure 39. Pelage color variation, radiation and metachromic bleaching along eumelanin and pheomelanin pathways depicted for all extra-Amazonian Howling Monkeys genus *Alouatta* of the Brazilian *Al. guariba* and *Al. caraya* Clades, and the Central-American *Al. pigra* and *Al. palliata* Clades.

Central American Black Howler *Al. pigra* is considered the most saturated eumelanin, least bleached, nearest to archetypic form of the *Al. pigra* and *Al. palliata* Clades. It is also by far the largest howling monkey. The *Al. palliata* Clade is believed to have diverged from ancestral *Al. pigra* about 3 MYA (Mittermeier et al., 2013). Taxon *Al. palliata* is sympatric with taxon *Al. pigra* in Tabasco State, Mexico and in a small part of Guatemala. From the Golden-mantled Howler *Al. palliata* radiating northwards derived the Mexican Howler *Al. mexicana*, and radiating southwards the South Pacific Blackish Howler *Al. aequatorialis*, ranging far south into the Pacific coastal forests of Colombia and Ecuador. There, it is sympatric with the Colombian Red Howler *Al. seniculus*. From *Al. aequatorialis* in SW Panama derived the Azuero Peninsula Howler *Al. trabeata* and the Coiba Island Howler *Al. coibensis* (Fig. 38).

During his long-term fieldwork on the ecology of all eight monkey species that occur in the Guianas, the senior author has repeatedly watched the basic principles of allopatric primate speciation at work. At his study site situated in pristine primary terra firme rain forest in Central Suriname, local populations of the Guianan Red Howler *Al. macconnelli* (Fig. 37), the most territorial among all extant howling monkeys when measured by the size of the hyoid bone, had passed beyond the howler's optimal densities (Van Roosmalen, 2013a; 2015). This was measured by the high frequency of dawn chorus and vocal battles of neighboring groups throughout the day and nighttime in the proximity of territorial boundaries. One day, a subadult male got pushed out of his parental group that ranged close to the campsite area. For several days after being expelled, this young howler male got repeatedly involved in vocal battles with neighboring groups that subsequently chased him out of their respective territories. Weeks later, far away from the campsite, a boundary conflict took place that seemed never ending. The researcher rushed over to the spot. He arrived just in time to witness this very subadult male being attacked by the leader of a resident group in the company of his harem. The whole group chased the young male into an isolated tree close to where he could watch the scene. The subadult male was in the company of a female he presumably had attracted ('stolen') from some resident group that had chased him out earlier. In an

attempt to escape from his attackers, the howler male almost fell out of the canopy. He just could get hold on a thick branch and was hanging underneath it only secured by the grip of his hands and tail. Then, they all began to bite in his hands and tail tip. With a scream, he let loose and came crashing over forty meters down to the forest floor, hitting it at a hair width away from the researcher's head. The monkey looked dead, his motionless body covered with blood. After a few minutes, however, he got back on his feet and slowly climbed up a small tree. Back in the canopy, he sat next to his mate that had been watching the show from a distance. The pair was never seen again within the borders of the 400-ha study area. Some time later, vocal battling recommenced. It came from the same direction, sounding only much farther away. In retrospect, we assume that the couple survived and in the long run found a place to settle down, start a family, and defend a small territory squeezed between the territories of some resident howler groups far away from their respective parental groups. One may speculate that the howler pair, driven by the trend to allopatry, also may have survived by venturing into some 'empty', marginal, or for howlers unfamiliar habitat. Or, in case the male was expelled from his parental group for his skin or (part of) coat color being somewhat lighter, he could have joined other outcast males that were discriminated upon and pushed out of their parental groups for other mutant metachromic deviances of skin and/or coat characters. For the sake of survival alone, such healthy young individuals may join efforts to stay alive. Together, they may turn into potential founder-colonies venturing into new lands, where they can thrive and reproduce unrestrictedly. At least as long as those lands, in turn, do not reach the taxon's optimal population density. By the time they do so, the generally accepted phenotype of that new parapatric or allopatric taxon or (eco)-species will have been stabilized while showing whatever features of further metachromic bleaching and/or depilation.

Living on an island in the Coppename River at about ten km from his field site, the senior author has repeatedly witnessed the coming and going of small groups of potential howler-founders to and fro Foengoe Island after having been forcefully pushed out from some mainland territory by the ruling group male(s). Pushed against the riverbank, they apparently did overcome their natural fear of water



and then swam toward the island. For some time, such immigrants tried to make a living on the island. Until it became clear to them they were trapped on an island too small to sustain a howler group year-round. Occasionally, such groups were spotted later while ranging along the opposite riverbank. We assume they had traversed the river swimming. Interestingly, a female howler that was raised as a pet and then set free to range across the 30-ha island, was eager to join any howlers coming onto the island. Sadly, when the immigrants eventually swam back to the mainland in search of new lands, the female stayed back on the island. Perhaps, she did so for lack of sufficient bonding or for fear of swimming across the river.

Capuchin Monkeys (genera *Cebus* and *Sapajus*) have diverged from Squirrel Monkeys (*Saimiri*) about 15 MYA. They formed distinct monophyletic

Clades that diverged during the Late Miocene to Early Pliocene, about 6.2 MYA. The Clades diversified during the Plio-Pleistocene era into two groups: Gracile or Untufted Capuchins (genus *Cebus*) in what is today the western Amazon, about 2.1 MYA, and Robust or Tufted Capuchins (genus *Sapajus*) in what are today SE Brazil, E Paraguay, and N Argentina, beginning about 2.7 MYA (Mittermeier et al., 2013). Gracile Capuchins genus *Cebus* are separated into the following five cladistics Groups or Clades: Humboldt's White-fronted Capuchin *Ce. albifrons* with four+ taxa (*Ce. albifrons*, *Ce. yuracus*, *Ce. unicolor*, and *Ce. cuscinus*), Guianan Weeper Capuchin *Ce. olivaceus* with three taxa (*Ce. brunneus*, *Ce. olivaceus*, and *Ce. castaneus*), White-faced Capuchin capucinus with two taxa (Colombian White-faced Capuchin *Ce. capucinus* and Panamanian White-faced Capuchin *Ce.*

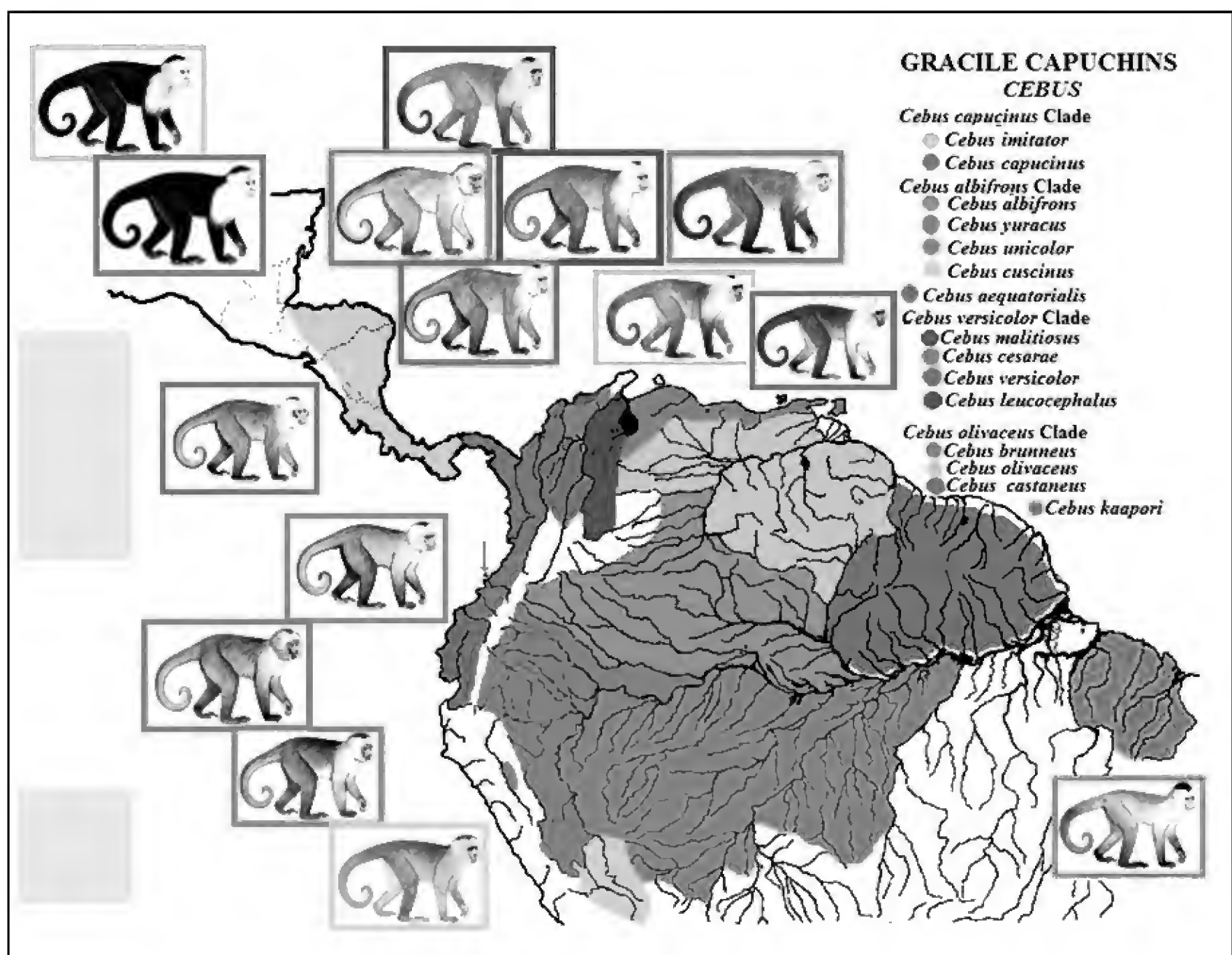


Figure 40. Distributions, allopatric speciation, radiation, and pathways of metachromic bleaching in all hitherto recognized Gracile Capuchins of the five distinguished phylogeographic Clades: *Cebus capucinus*, *C. olivaceus*, *C. versicolor*, and *C. albifrons*. The fifth Clade *C. aequatorialis* is monotypic.



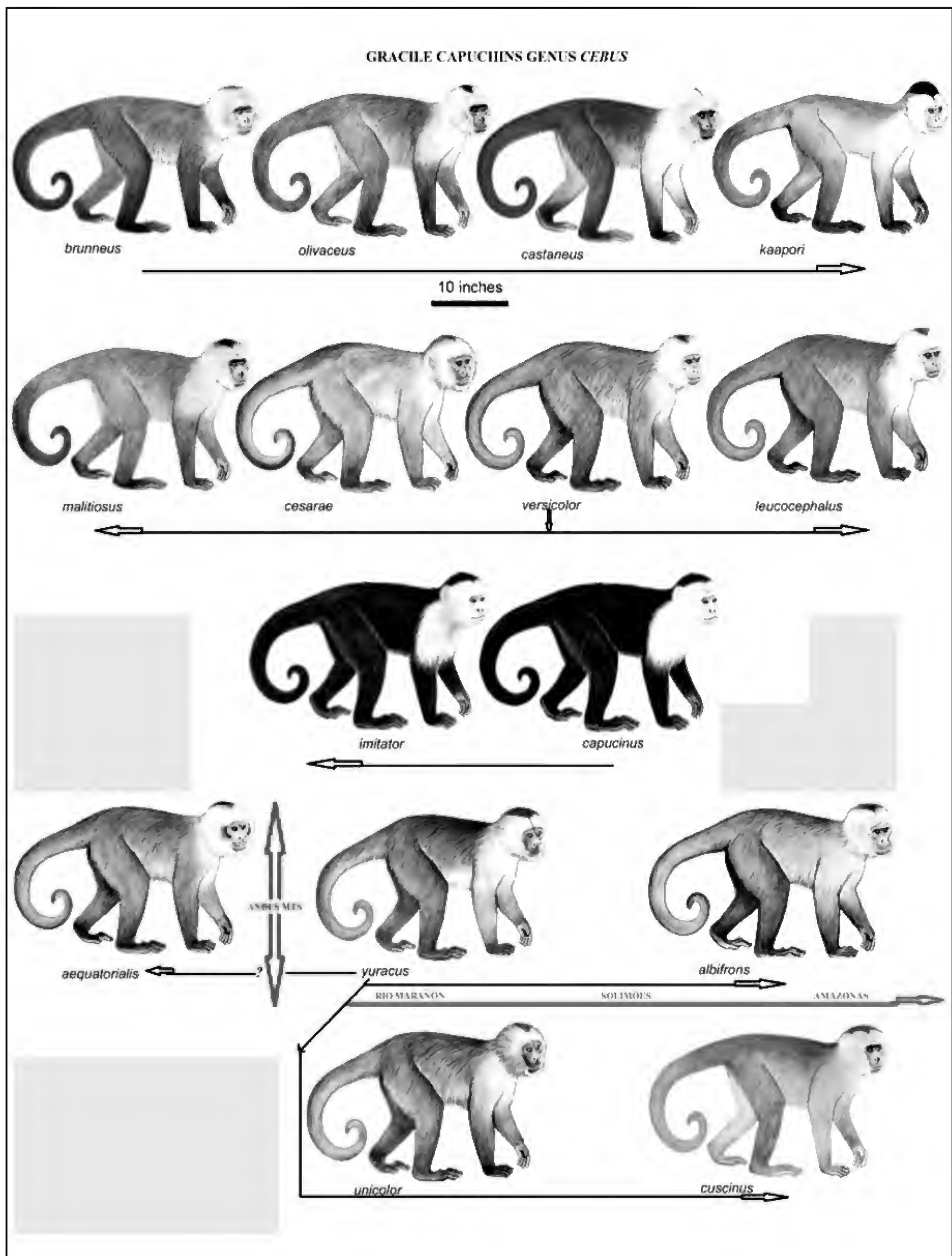


Figure 41. Metachromatic diversification along eumelanin and pheomelanin pathways of metachromatic bleaching (arrowed lines), speciation and radiation in all hitherto recognized Gracile Capuchins (*Cebus*) of the five distinguished phylogeographic Clades: *Cebus olivaceus*, *C. versicolor*, *Cebus capucinus*, and *C. albifrons*. *Cebus aequatorialis* from W Ecuador and NW Peru is monotypic, but may have derived from ancestral *C. yuracus* that once traversed the Andes Mts.

*imitator*), and Varied White-fronted Capuchin *Ce. versicolor* with four taxa (*Ce. versicolor*, *Ce. leucocephalus*, *Ce. cesarae*, and *Ce. malitiosus*). The recently discovered Ka'apor Capuchin *Ce. kaapori* ranging S of the lower Rio Amazonas is geographically closest related to the Guianan Weeper Capuchin (i.e., taxon *Ce. castaneus* ranging along the left/north bank of the lower Rio Amazonas) and, therefore, may form a sister Clade to it (Figs. 40, 41).

Within the *Ce. capucinus* Clade we consider the Colombian White-faced taxon *Ce. capucinus* (ranging from E Panama, through W Colombia south as far as NW Ecuador), the nearest to archetypic, least metachromic bleached form. Its body, crown, limbs, and tail are black. The chest is white, extending forward to the face and front of the crown and upward to the shoulders and upper arms. The Gorgona White-faced Capuchin *Ce. curtus curtus* is a small and relatively short-tailed subspecies from Gorgona Island sitting on the Colombian Pacific coast. From taxon *Ce. capucinus* derived *Ce. imitator*, the taxon that ranges from N Honduras, C and W Nicaragua, Costa Rica south into W Panama. It resembles much the typical Colombian White-faced Capuchin *Ce. capucinus*, but females have elongated frontal tufts with a brownish tinge.

Within the *Ce. olivaceus* Clade we consider the Venezuelan Brown Capuchin *Ce. brunneus* from N Venezuela east of the Sierra de Perijá and along the Coastal Range, including the island of Trinidad (where it is possibly introduced), the nearest to archetypic, least metachromic bleached form. Its pelage is thick and long, the upperparts are generally darker along the middle of the back than on the sides, the hairs are dusky basally, with a broad zone of chestnut in the middle, and black at the tips. Face and sides of the head are pale yellowish gray. The crown has a broad V-shaped patch of long hairs, narrowing to a point in front of which a narrow black line runs forward to the nose. Chin and lower parts of cheeks are grayish or fulvous white to whitish. Underparts are blackish brown, with tips of the hairs hazel. The throat is lighter than the chest and belly. Upper arms are maize yellow. Outer forearms are blackish with yellowish tips, inside forearms are much darker. Hands are blackish, hindfeet are nearly black. Tail is colored as back. From ancestral *Ce. brunneus* derived the Guianan

Weeper Capuchin *Ce. olivaceus* that is restricted to the Venezuelan Amazon Basin in forests of the Guayanian Shield, from the upper Río Orinoco east to the left bank of the Rio Essequibo in W Guyana. Its pelage is overall dark brown or reddish with black-agouti banding on flanks, limbs, and tail. The face is naked and pink. Cheeks are buffy-white. It differs from *Ce. brunneus* in the advanced bleached albinotic head and upper arms and the wider V-shaped black crown cap.

From ancestral *Ce. olivaceus* derived the Chestnut Weeper Capuchin *Ce. castaneus*. This taxon ranges from the Rio Essequibo E through Suriname and French Guiana into N Brazil, where its distribution is delineated by the Rios Negro, Branco, and Catrimani in the W, Rio Amazonas in the S, and the Atlantic coast in the E (it also inhabits Caviana and Mexiana Islands in Amazon's estuary). It differs from *Ce. olivaceus* in the narrower black triangle on the crown and the pelage of the head being overall yellowish-white, but reddish-chestnut above the ear and nape, in the advanced pheomelanin bleached reddish-chestnut upperparts of the body and limbs, and pale yellow shoulders and fronts of arms above the elbows. A founder-colony of the Chestnut Weeper Capuchin *Ce. (olivaceus) castaneus* must once have traversed the lower Rio Amazonas. From it derived the Ka'apor Capuchin *Ce. kaapori* that ranges in NE Brazil south of the lower Amazon River (NE Pará and NW Maranhão). This taxon is characterized by a longer body in comparison to other *Cebus* species. It is grayish agouti-brown, and lighter on the flanks. Face, shoulders, mantle, and tail tip are silvery-gray, the limbs are agouti, and the hands and feet dark brown or black. The crown has a triangular black cap that extends to a dark stripe down the nose. The pelage of the Ka'apor Capuchin is overall advanced eumelanin bleached to nearly albinotic, as such much contrasting with the saturated eumelanin blackish crown cap, hands and feet. Being phylogeographically farthest radiated away from the center of dispersion (NW Venezuela) of the *Ce. olivaceus* Clade, and occupying a dead-end distribution, where it also has to compete with the Guianan Brown Capuchin *Sapajus apella* (Figs. 42–44), *Ce. kaapori* is clearly the most progressively bleached, near-albinotic taxon within the *Ce. olivaceus* Clade (Fig. 41).

Within the *Ce. versicolor* Clade we consider the Varied White-fronted Capuchin *Ce. versicolor* the

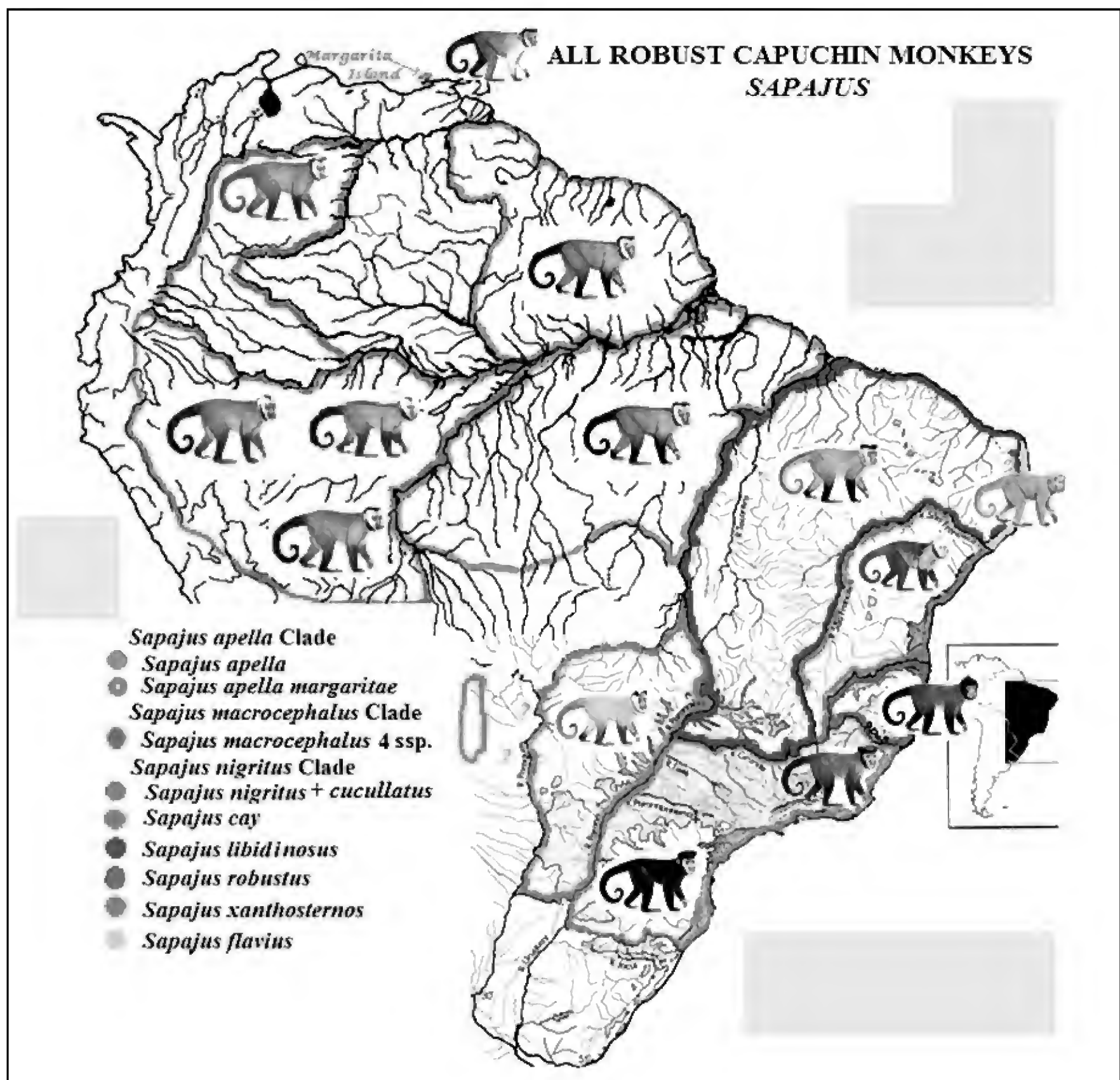


Figure 42. Phylogeography, allopatric speciation, radiation, and pathways of metachromic bleaching followed in all hitherto recognized Robust (Tufted) Capuchins of the three distinguished phylogenetic Clades: *Sapajus nigrinus*, *S. apella*, and *S. macrocephalus*. From an ancestral saturated eumelanin (all-black) form of the *S. nigrinus* Clade, quite recently (an estimated 400,000 YA) radiated away into the Amazon the pheomelanin bleached species *S. apella* (including the insular taxon *S. a. margaritae*), and *S. macrocephalus*, the latter with four different taxa/'species-in-the-making' - from SE to N: *juruanus*, *pallidus*, *maranonis*, and *fatuellus*).

nearest to archetypic, least metachromic bleached taxon. It is distributed in N Colombia in the middle Río Magdalena Basin. It is the darkest among the Clade's four taxa, though a rather pale form with red tones on the mid-dorsal region and foreparts of the limbs, generally contrasting with the rest of the body (Fig. 41). From *Ce. versicolor* derived towards the NE the Sierra de Perijá White-fronted Capuchin *Ce. leucocephalus* that ranges in N Co-

lombia from the W slope of the Cordillera Oriental E to the Ríos Zulia and Catatumbo Basins and NW Venezuela (Zulia State). This taxon is progressively bleached, near-albinotic in the head, chest, and shoulder parts. From *Ce. versicolor* derived towards the N first the Río Cesar White-fronted Capuchin *Ce. cesarae*, ranging in N Colombia, in the Río Cesar Valley, W into the S and E slopes of the Sierra Nevada de Santa Marta. From taxon *Ce. cesarae*,

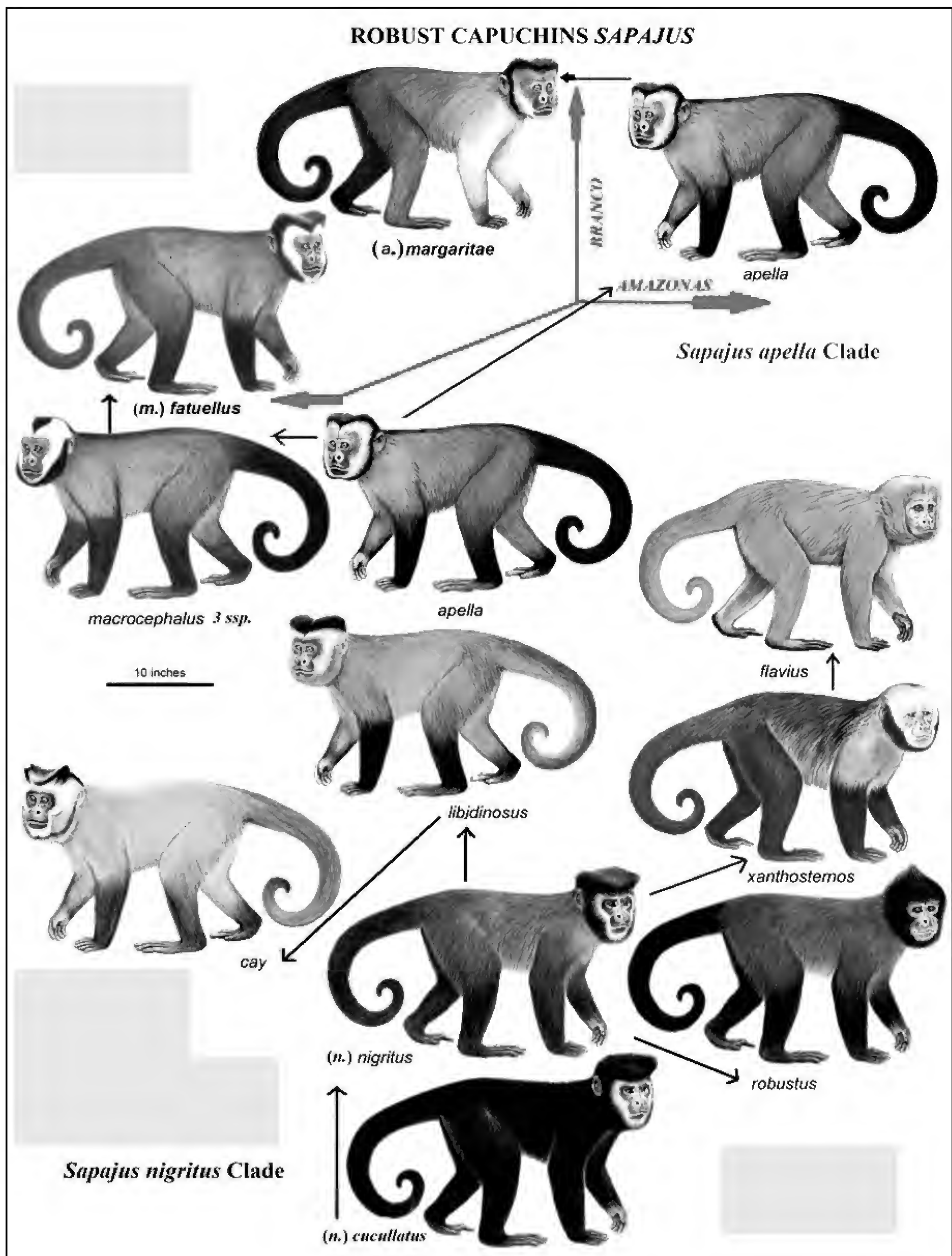


Figure 43. Radiation and metachromic diversification in the *Sapajus nigrinus* and *S. apella* Clades of Robust or Tufted Capuchins. From an ancestral saturated eumelanin form of *S. nigrinus* the species *Sapajus apella* and *S. macrocephalus* radiated away into the Amazon with different taxa 'in-the-making'.



in turn, derived the Santa Marta White-fronted Capuchin *Ce. malitiosus* that is only known from the NW base of Sierra de Santa Marta. It may range also throughout the lower W and N slopes of the Sierra Nevada in N Colombia. The two taxa are the palest among the N Colombian and Venezuelan White-fronted Capuchins. Taxon *Ce. cesarae* is buffy in the head and throat parts and pheomelanin bleached orangish in the cap, middle of the back, forearms, and forelegs, as such contrasting with the sides of back and trunk. Taxon *Ce. malitiosus* is advanced eumelanin bleached in the silvery to cinnamon-brown chest and belly, and a contrasting albinotic area of the front extending well over the upper surfaces of the shoulders and inner sides of upper arms (Fig. 41).

Within the *Ce. albifrons* Clade we consider the Mara  n White-fronted Capuchin *Ce. yuracus* the nearest to archetypic, overall least metachromic bleached taxon (Fig. 41). This taxon is distributed north of the Amazon River in S Colombia, E Ecuador, NE Peru, and presumably W Brazil between the Rios I   and Solim  es. It is gray-fronted on the forehead, sides of the face, chest, and outer sides of the arms. Its general color is ochreous-brown, contrasting sharply with the grayish to buffy outer sides of forelimbs, and with the pale silvery to orangish underparts. The cap is black, with a median line running down inbetween the eyes. The tail is brown like the back, but paler towards the tip. From ancestral *Ce. yuracus* derived first Humboldt's White-fronted Capuchin, the nominate taxon *Ce. albifrons* that is widely distributed across the upper Amazon Basin of S Venezuela, S and E Colombia (occurring north of the Rio Amazonas and the R  o I  -Putumayo, N as far as the R  o Meta, and in the lowlands W of the Orinoco, and NW Brazil (N of the Rio Solim  es, and W of the Rios Negro and Branco, as far north as the Rio Uraricoeira). Humboldt's White-fronted Capuchin *Ce. albifrons* is overall pale grayish-brown, darker on the limbs. Hands and feet are yellowish-brown. The tail is ashy above, whitish below, and brownish-black towards the tip. The front is creamy white, and there is a cap of short dark fur on the crown that is rounded in the front and well demarcated from the light-colored forehead. The face is naked and pinkish, flesh-colored. From *Ce. yuracus* derived also Spix's White-fronted Capuchin *Ce. unicolor*, most likely after a founder-colony of ancestral *Ce.*

*yuracus* traversed the upper reaches of the R  o Ucayali in E Peru. It is nowadays widely distributed in the upper Brazilian Amazon Basin, south of the Amazon River and west of the Rio Tapaj  s, throughout the northern parts of Mato Grosso and R  ndonia States, and throughout the Rios Madeira, Pur  s, Juru  , and Javar   Basins as far west as the R  o Ucayali. *Cebus unicolor* is uniformly bright ochreous or grayish-brown with darker grayish-brown flanks and mid-back, with a yellowish or cream-white front and reddish-yellow to reddish limbs and tail. From ancestral *Ce. unicolor* derived later the Shock-headed Capuchin *Ce. cuscinus* that is believed to range from the right bank of the upper reaches of the Rio Pur  s in SE Peru, W into the Cuzco Department including the upper R  o Madre de Dios, and S and E as far as the R  o Tambopata Basin, also extending into NW Bolivia. Taxon *Ce. cuscinus* has a longer, silkier fur than *Ce. unicolor* and is less brightly colored. Its limbs are browner and contrast less with the back. The cap is large, distinct, and dark brown. The forearms are orange-rufous on the outside, darker on the wrists and hands. Underparts are ochreous-orange and silvery, becoming buff on the chest. The fronts of the shoulders and inner sides of the upper arms are whitish. The tail is brown, somewhat paler towards the tip. The male has a broad pale frontal region sharply defining the dark-brown cap. Overall, *Ce. cuscinus* is the most advanced pheomelanin bleached taxon of the *Ce. albifrons* Clade. It is the form that radiated away farthest from the center of this Clade's dispersion (Fig. 40). The Ecuadorian White-fronted Capuchin *Ce. aequatorialis* is monotypic. It may form a sister Clade to the Gracile Capuchins from the upper Amazon Basin. Ancestral Mara  n White-fronted Capuchin *Ce. yuracus* once must have traversed the Andes Mountains somewhere at the upper reaches of the R  o Mara  n and then diverged into *Ce. aequatorialis*. *Cebus aequatorialis* is distributed in Ecuador and NW Peru, in the lowlands west of the Andes (Fig. 34). Its upperparts are pale cinnamon rufous, darker along the midline of the back. Front and sides of the head are yellowish white, with a narrow black transverse line on the forehead forming the cap, from which a narrow median black line descends to the nose. Hands and feet are a little darker, more brownish than the arms and legs. The chest is lighter than the belly (Fig. 41).



During long-term fieldwork in Central Suriname, the first author spotted a few times by chance small parties consisting of phenotypically deviant cream-white, long-haired, fluffy-coated males of the Guianan Weeper Capuchin *Ce. (olivaceus) castaneus*. Such all-male parties seemed to range randomly while travelling at high speed through the vast landscape of pristine matrix lowland rain forest in the middle of which his study area was situated. It is located at more than one-hundred km north of Kaiser Mountains, a hilly country of which the foothills seem to form the Guianan Weeper Capuchin's core distribution. This region that provides this monkey with its preferred habitat - 'mountain savanna forest' - was found to sustain a very large population of this elsewhere in the Guianas extremely rare taxon *Ce. (olivaceus) castaneus*. Mountain savanna forest is typified by an understory that is dominated by the majestic 'bergimaripa' palm *Attalea speciosa* Mart. (Arecaceae). Above 400 m altitude, this palm tree is locally so abundant that one gets the impression to walk through a monocultural plantation of the African oil-palm *Elaeis guineensis* Jacq. (Arecaceae). The large fruits of *Attalea speciosa* constitute the Guianan Weeper Capuchin's principal daily food throughout most of the year. Mountain savanna forest above 400 m altitude, therefore, may function as a 'keystone habitat' to the Guianan Weeper Capuchin, hence the high population density.

Two decades later, while conducting biodiversity surveys in Pico da Neblina National Park situated in the extreme northwestern corner of the Brazilian Amazon, the authors spotted a population of near-albinotic Weeper Capuchins that were characterized by a very dense, fluffy, overall long-haired, cream-white bleached fur. Their coat features looked very similar to that of the all-male parties that were seen sporadically passing through the Voltzberg study area. The Pico da Neblina population of weeper capuchins was spotted in a low type of cloud forest scrub that grows at high altitudes of 2,000 to 2,500 m. To the astonishment of the researchers, the capuchins were seen spending part of the daytime on the ground in the middle of open tepu  (sandstone table-mountain) 'rock savanna'. They were seen foraging for invertebrates, mostly snails, other organisms endemic to tepu  mountain tops, in addition to vegetable matter (e.g., roots, tubers and pseudobulbs of all sorts of

terrestrial bromeliads and orchids). In retrospect, our sighting may be explained for as follows. In the past, a founder-colony of near-albinotic Guianan Weeper Capuchins, driven by the 'trend to allopatry' out of the center of dispersion of archetypic *Ce. (olivaceus) castaneus*, may have traversed the upper Rio Branco and then reached the Pico da Neblina area. The latter is situated somewhat south of the R o Cassiquiare, the channel that runs through the watershed connecting the basin of the Rio Negro with that of the R o Orinoco. The fully bleached euchromic, long-haired, soft-coated weeper capuchins that were seen foraging in tepu  cloud forest and open rock-savanna at 500–1,000 m below the 3,004 m Pico da Neblina summit much resembled the near-albinotic, fluffy-coated *Ce. (olivaceus) castaneus* from Kaiser Mountains, Central Suriname. If the Pico da Neblina population turns out to represent a new taxon or one in-the-making, the 'Neblina Weeper Capuchin' would occupy a dead-end distribution in the southwesternmost corner of the *Ce. olivaceus* Clade's range, the farthest away from the supposed center of the Clade's dispersion (the Guianas or Venezuelan Coastal Range). The upper Rio Negro forms the division between the distributions of the Guianan Weeper Capuchin *Ce. olivaceus* Clade and the Humboldt's White-fronted Capuchin *Ce. albifrons* Clade (Fig. 39). This example from the field is in line with our theory of allopatric speciation in male-defended territorial primates such as *Cebus*. The 'Neblina Weeper Capuchin' may have radiated away from the *Ce. olivaceus* Clade's center of dispersion in the Guianas following a pathway of metachromic bleaching driven by the trend to allopatry in phenotypically deviant euchromic, long and fluffy-haired males. Interestingly, the mechanism of allopatric speciation and radiation of a monophyletic clade of monkeys like that of Humboldt's Weeper Capuchins at first sight seems non-adaptive, at least in strict Darwinian sense, for it is solely based on discriminatory behavior performed exclusively by high-ranking males. The genes for warm, long and fluffy-haired coats are simply retained in the genes of these capuchin 'founder-colonies'. Such a feature would therefore not a priori be the result of adaptive processes of natural selection. Its warm coat only secondarily happened to have survival value. It only turned adaptive when these gracile capuchins had to adapt in a short

period of time to a new habitat or feeding niche that would not have suited the species they derived from. Following this rationale, one may speculate about a similar metachromic pathway that our hominid ancestors about 6 MYA must have followed when exchanging the canopy of tropical rain forest for a landscape of arid, open savanna scrub. Or a similar pathway of metachromic bleaching towards albinotic (from a black to yellow or white skin color) and/or depilation of the body that different hominids followed between 100,000 and 50,000 years ago, when the trend to allopatry (male discriminatory behavior) forced them to leave the center of hominid dispersion and the cradle of hominid evolution - C and N Africa - to make a harsh living of nomadic big-game hunting/gathering in (for hominids) climate - and habitat - wise new, marginal, unsuitable, or inhospitable landscapes of Central Europe, the Middle-East and SE Asia.

Capuchin Monkeys of the genera *Cebus* and *Sapajus* formed distinct monophyletic Clades that diverged during the Late Miocene to Early Pliocene, about 6.2 MYA. During the Plio-Pleistocene era the Clades diversified into two groups: Gracile or Untufted Capuchins genus *Cebus*, about 2.1 MYA in what is nowadays the western Amazon, and Robust or Tufted Capuchins genus *Sapajus*, beginning about 2.7 MYA in what are today SE Brazil, E Paraguay, and N Argentina. There is strong evidence from molecular genetic studies that Robust Capuchins (genus *Sapajus*) spent most of their evolutionary history in the Atlantic Forest of SE Brazil, NE Argentina, and E Paraguay. And that the current wide-ranging sympatry of Robust and Gracile Capuchins across the larger part of the Amazon Basin is the result of a single, rapid, Late-Pleistocene invasion of Robust Capuchins from the Atlantic Forest, first into the 'Cerrado' and 'Cerradão' of C and NE Brazil, and only recently (about 0.4 MYA) from central South America north into the Amazon Basin and the Guianas (Mittermeier et al., 2013). Though widespread throughout the Amazon Basin and the Guayanian Shield, the genetic differentiation of the Amazonian Robust Capuchins is limited. The fact that the phenotypic diversity of the Amazonian Robust Capuchins is not mirrored by a corresponding genetic diversity strongly supports our theory of allopatric primate speciation. A number of the 16 taxa that are overall recognized in

different taxonomic arrangements (e.g., Groves, 2001a; Silva Jr., 2001; Silva Jr., 2002) may well represent taxa 'in-the-making'. Here, we follow Silva Jr. (2001) in recognizing only two species: the Guianan Brown Capuchin *Sap. apella* with three subspecies distributed in the eastern Amazon and the Guianas, and the Large-headed Capuchin *Sap. macrocephalus* with four subspecies that are distributed across the western Amazon. These taxa form two monophyletic Clades in which little genetic differentiation is shown. In contrast, the non-Amazonian species recognized by Silva Jr. are genetically distinct forming the monophyletic *Sap. nigrinus* Clade (Figs. 39, 40). Among the six species of the extra-Amazonian *Sap. nigrinus* Clade we consider the Black-horned Capuchin *Sap. nigrinus* the nearest to archetypic, less bleached species (Figs. 42, 43). Its southernmost populations representing the darkest, overall most saturated eumelanin form may well be a distinct taxon named *Sap. cucullatus* by Spix in 1823. The Black-horned Capuchin is the most S occurring of all robust capuchins. It is distributed in SE Brazil, S of the Rios Doce and Grande, extending S through the Atlantic Forest, and taxon *Sap. cucullatus* further south E of the Rio Paraná into Rio Grande do Sul State and NE Argentina. The Black-horned Capuchin is a large-sized species with horn-like tufts on either side of the head at the temples. Its fur is overall very dark brown or grayish in *nigrinus*, and black in *Sap. cucullatus*, often with slightly pheomelanin bleached, reddish or yellow-fawn colored underparts. A black to dark-grayish crown (with tufts in adults) contrasts much with the light colored face. The tail is black. From *Sap. nigrinus* derived the monotypic Crested Capuchin *Sap. robustus* after a founder-colony of *Sap. nigrinus* traversed the Rio Doce to the north. It is distributed in SE Brazil from the Rio Jequitinhonha in Bahia State S to the Rios Doce and Suaçuí Grande in Espírito Santo State and E Minas Gerais State, E of the Serra do Espinhaço. This taxon is very dark wood-brown or blackish above and on the limbs, with a faint dorsal stripe. The underparts are pheomelanin bleached red or yellowish, whereas forearms, hands, lower legs, and feet are deep dark brown to black. Its face is dark grayish, with some white hairs on the forehead and temples. The crown tufts are tall and conical in shape. From a founder-colony of the northern Black-horned Capuchin *Sap.*

*nigritus* that once traversed the Rio Jequitinhonha to the north, derived the Yellow-breasted Capuchin *Sap. xanthosternos*. Yellow-breasted Capuchins tend to be much darker in overall color in the southwestern part (N Minas Gerais State), whereas they are pale in the northern part of this taxon's distribution. The monotypic taxon *Sap. xanthosternos* is further distributed in CE Brazil, S and E of the Rio São Francisco, south to the Rio Jequitinhonha (in S Bahia State). It is generally pheomelanin bleached brindled reddish above with a sharply marked, golden-red underside. Tail and limbs remained saturated eumelanin black. Its crown does not contrast with the body, the cap is black, and the face and temples are fawn. It has small backward pointing tufts. From Yellow-breasted *Sap. xanthosternos* derived the monotypic Blond Capuchin *Sap. flavius*, which was described by Schreber in 1774. Until it was collected in 2005, the Blond Capuchin was only known from an early illustration. Before colonial times, it must have been distributed in Coastal NE Brazil from S Rio Grande do Norte State through Paraíba State into NE Pernambuco. This taxon may extend its range to the left bank of the Rio São Francisco in Alagoas State. The Blond Capuchin is small, distinctive, and untufted. Its body and limbs are uniformly advanced pheomelanin bleached golden-yellow, whereas its lower-body parts are slightly darker golden-yellow. Hands and feet are black, whereas the tail is uniformly golden-blond, but darker on the dorsal side than the rest of the body. It further has a rectangular snow-white cap on the front of the head, to just above the ears, and a furless, pendulous throat flap. Face and forehead are near-albinotic, cream to pinkish colored, the eyes are brown. *Sapajus flavius* occupies degraded Coastal Atlantic Forest and *Montrichardia linifera* (Arruda) Schott (Araceae) swamp in Pernambuco State, and 'caatinga' scrub in W Rio Grande do Norte State. Being advanced pheomelanin bleached to near-albinotic, taxon *flavius* occupies a dead-end distribution. It therefore fully concurs with our theory on the origin of allopatric speciation. The theory suggests that a founder-colony of progressively pheomelanin bleached *Sap. xanthosternos* once was forced to make a living in the (for Robust Capuchins) marginal or unsuitable habitat of swamps and low xerophytic, spiny scrub of profusely branched bushy vegetation up to 8–10 m in height, mixed

with prickly succulent cacti, and spiny, rigid-leaved bromeliads. Blond Capuchins are reported to use even sand dunes and mangroves.

From the northern form of the Black-horned Capuchin derived to the W the Hooded Capuchin *Sap. cay*, and to the N the Bearded Capuchin *Sap. libidinosus* (Fig. 42). The monotypic taxon *cay* is distributed in SE Bolivia, N Argentina, SW Brazil - W of the Rio Paraná through Mato Grosso State into SW Goiás and Mato Grosso do Sul - and Paraguay (E of the Río Paraguay as far as the Río Paraná). The Hooded Capuchin *Sap. cay* is a small, short-limbed species without sexual dimorphism, typified mainly by its prominent dark dorsal stripe. *Sapajus cay* is very variable in color, but generally rather pale. Its crown is pale to blackish-brown, with two small hornlike tufts. Dorsal parts of the body (shoulders, front of the upper arms, saddle, rump, and thighs) are grayish-brown. Forearms, hands, wrists, lower legs, and feet are blackish. Eyes, nose, and mouth are surrounded by white hairs. It has a small white beard, and a dark line extends down from the ears to under the chin. From the Black-horned Capuchin derived to the north the monotypic Bearded Capuchin *Sap. libidinosus*. This taxon is distributed in C and NE Brazil, W and N of the Rio São Francisco into Maranhão State, and in the W of Piauí State, and E to C Rio Grande do Norte, NW Paraíba, W Pernambuco, and W Alagoas; to the W it extends to the Rio Araguaia, and its southern limit is the north bank of the Rio Grande in Minas Gerais. To the west, the Bearded Capuchin taxon *Sap. libidinosus* is replaced by *Sap. apella*, to the east by *Sap. flavius*, and to the south of the Rio São Francisco by *Sap. xanthosternos*. *Sapajus nigritus* occurs just south of the Rio Grande. Some hybridization between *Sap. libidinosus* and *Sap. nigritus* is reported to occur in the western part of Minas Gerais. The Bearded Capuchin *Sap. libidinosus* is comparatively small and does not show sexual dimorphism. It differs from all other Robust Capuchins by the rusty-red hair on the back of the neck, the dark-brown preauricular stripe running down the side of the face in front of the ears, and the orange-yellow throat and dorsal parts of the body, flanks, outer part of arms, and proximal two-thirds of the tail. Forearms are dark, and the lower back and outer surface of thighs are grayish-brown, mixed with some reddish hairs. The crown is black, with rounded, sometimes bushy, black tufts.

Here, we recognize only two Amazonian Robust or Tufted Capuchins (genus *Sapajus*): the monotypic Guianan Brown Capuchin *Sap. apella* that is distributed in the eastern Amazon and in the Guianas, and the Large-headed Capuchin *Sap. macrocephalus* with a number of forms/morphs/subspecies that are distributed throughout the western Amazon as far north as the Magdalena Valley in N Colombia (Fig. 42). Taxon *Sap. apella* is found in the rain forests of the Amazon Basin of Brazil N of the lower Rios Negro and Amazonas, E of the Rio Branco, extending N to the southeastern part of the Orinoco Delta in Venezuela and the Guianas. Its distributional limits in the S, SE, and E are defined by the extent of the Amazon rain forest, in the S and E of Maranhão State marking the transition zone to xeric deciduous forest and 'caatinga' scrub. In the West, its distribution is limited by the interfluvium of

the Rios Negro and Solimões and the Rio Madeira Basin. The Guianan Brown Capuchin species *Sap. apella* is relatively large and heavily built, with a broad head, flat face, and short limbs. Its coat is long and coarse, with all five extremities darker colored than the rest of the body. It is generally gray-fawn to dark brown above, with a yellowish or red underside. The lower limbs and tail are black, and there is a variably distinct dorsal stripe. The face and temples are light gray-brown. The crown tuft is black and forms short tufts above the ears (the characteristic 'horns'). The crown cap extends down the cheeks forming 'sideburns' that often meet below the chin. There is no sexual dimorphism, but males are slightly heavier and often overall much darker colored. The Margarita Island Capuchin taxon *Sap. apella margaritae* that is endemic to Isla de Margarita off the Caribbean coast of Venezuela

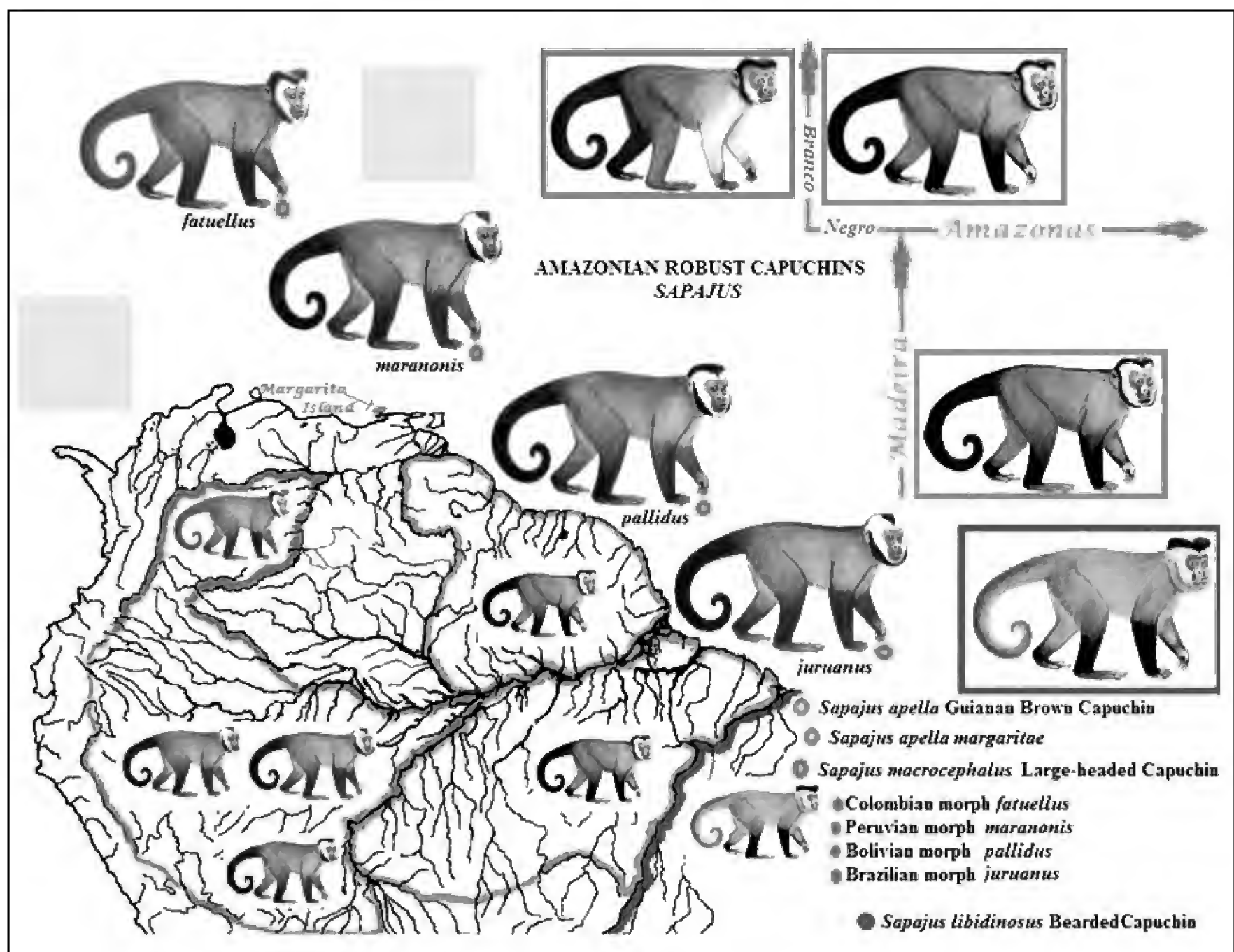


Figure 44. Phylogeography, allopatric speciation, and metachromic bleaching in all Amazonian Robust Capuchins disputedly divided up in *Sapajus apella* and *S. macrocephalus*, the latter with different taxa 'in-the-making'.



distinguishes itself from the nominate Guianan Brown Capuchin by longer dark sideburns in front of the ears, and progressively bleached, pale-yellow or straw colored, near-albinotic upper arms and shoulders. The thighs and rump are pale yellow-brown, and flanks, lower back, and upper chest are pale brown, becoming paler from the upper back to the neck. The face is grayish, tinged pink on the cheeks and chin. The black cap extends in a “V” to between the eyes, with small round tufts above the eyes.

The monotypic Large-headed Capuchin taxon *Sap. macrocephalus* is distributed in the western Amazon Basin, but its taxonomy and distributional limits are poorly defined. According to Silva Jr. (2001) this species includes the forms/morphs/subspecies *Sap. fatuellus* from the upper Magdalena Valley, Colombia, *Sap. maranonis* from Rio Ham-

burgo, Peru, *Sap. pallidus* from the Río Beni, C+N Bolivia, and *Sap. juruanus* from the Rio Juruá, Brazil. Preliminary genetic studies in 2012 failed to indicate that *Sap. apella* and *Sap. macrocephalus* were distinct taxa. Large-headed Capuchins are distributed across the upper Amazon Basin in E Colombia, north as far as the Río Arauca on the border with Venezuela, E Ecuador, E Peru, W Brazil, and C and N Bolivia (S at least as far as the upper Río Beni). Their overall coat color is gray-brown or ochreous to dark brown above, with a dark dorsal stripe, and yellow-fawn or red-gold below. Sides of the neck are lighter, upper arms are pale yellowish, and legs are black with yellow-fawn or red-gold below. Adults have high, pointed crown tufts that resemble horns, which become reduced with age. There is often a gray-white stripe running from eye to ear. Four forms of the Large-headed

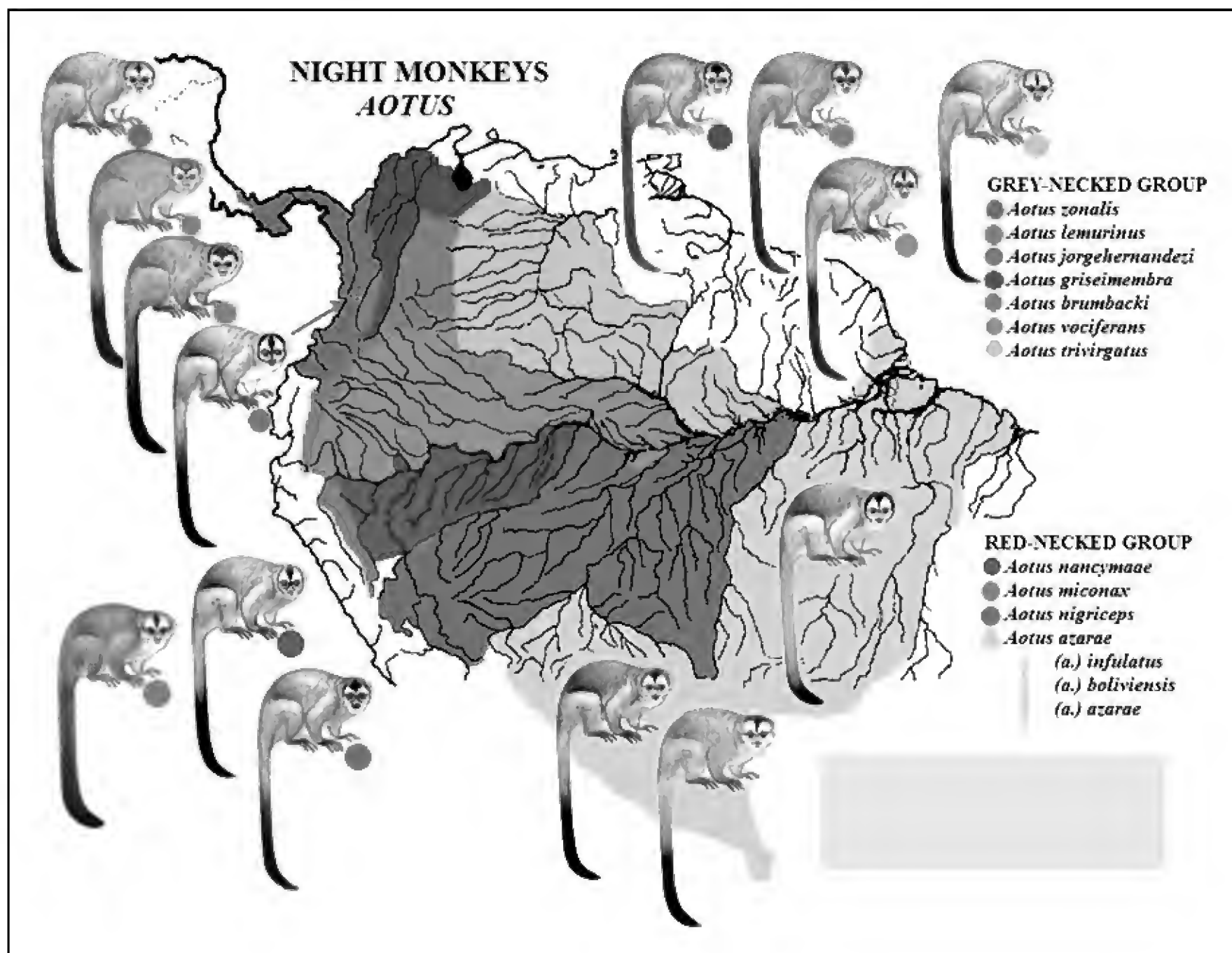


Figure 45. Phylogeography, allopatric speciation, radiation, and metachromic diversification in all hitherto recognized taxa of Night Monkeys, genus *Aotus*.



Capuchin have been distinguished (Fig. 44). The Colombian form *Sap. fatuellus* is bright brown above and red below, having a prominent dorsal stripe. Its face is almost naked and dark-purplish to flesh-colored. The Peruvian form *Sap. maranonis* is uniformly dark chestnut-brown above, becoming more reddish towards the flanks, and deep yellow-brown below. Its legs, tail, and (sometimes) forearms are black. Its cap is distinctly black, whereas temples and sides of the crown are often white. It has a crescent-shaped whitish patch above each eye. There are no crown tufts or they are minimal. The Brazilian form *Sap. juruanus* is reddish-brown above with a very distinct blackish dorsal stripe. The throat and upper chest are blackish or pale reddish-buff, and limbs and tail are dark brown or black. The Bolivian form *Sap. pallidus* from south of the Río Madre de Dios has also been referred to as a subspecies of *Sap. libidinosus*, but such taxonomy would be conflicting with our theory on allopatric speciation, for *Sap. libidinosus* from CE Brazil is overall more advanced pheomelanin bleached in comparison with *Sap. pallidus*. Both the Colombian morph/taxon *Sap. fatuellus* of the Large-headed Capuchin *Sap. macrocephalus* and the insular Margarita Island Brown Capuchin *Sap. apella margaritae* are in their overall advanced pheomelanin bleached coat coloration clearly following the metachromic pathway to albinotic, and therefore fully concur with our theory of allopatric speciation (Fig. 44).

Night Monkeys or Douroucoulis genus *Aotus* represent a very old lineage that is generally placed in a family of its own - Aotidae. The molecular genetic evidence classifies them as a subfamily of the Cebidae. There is also morphological evidence to place *Aotus* in the Pitheciidae. There are generally two Groups distinguished: the “Gray-necked Group” (characterized by grayish to brownish agouti sides of the neck and body), which occurs north of the Amazon River, and the “Red-necked Group” (characterized by partly or entirely orange or yellowish sides of the neck and chest, much contrasting with the grayish to brownish-agouti colored sides of the body), which occurs south of the Amazon River (Mittermeier et al., 2013). Recently, up to eleven species have been recognized, of which at least seven in the Gray-necked Group: the Lemurine Night Monkey *Ao. lemurinus*, the Panamanian Night Monkey *Ao. zonalis*, Brumback’s

Night Monkey *Ao. brumbacki*, the Gray-legged Night monkey *Ao. griseimembra*, Spix’s Night Monkey *Ao. vociferans*, Humboldt’s Night Monkey *Ao. trivirgatus*, and Hernández-Camacho’s Night Monkey *Ao. jorgehernandezi* (Figs. 45, 46). In the Red-necked Group are recognized four species: the Andean Night Monkey *Ao. miconax*, Ma’s Night Monkey *Ao. nancymae*, the Black-headed Night Monkey *Ao. nigriceps*, and Azara’s Night Monkey *A. azarae* (Figs. 45–47). Sexual dimorphism in night monkeys is absent. They are also not sexually dichromatic in coloration and facial markings. The coat is in metachromic sense primitive, archetypic saturated eumelanin, grayish to grayish-tan with a pheomelanin bleached, lighter tan or yellowish underside. In Red-necked species, ventral surfaces of neck, chest, abdomen, and inner sides of arms and legs are orangish or russet colored. The faces have white patches over eyes, topped by black stripes, and a triangular black patch running from the center of the forehead down between the eyes. Black stripes are also extending from the lateral side of each eye to the forehead, varying in width and darkness, and may or may not converge posteriorly with the central stripe. Tails are generally agouti-brown, distally black-tipped. Night Monkeys most likely descended from a diurnal haplorrhine. They only are secondarily nocturnal and have retained their color vision.

Within the Gray-necked Clade *Ao. lemurinus* is the nearest to archetypic, saturated eumelanin, less bleached taxon. It is a montane species of the Colombian Andes range, at elevations above 1,000–1,500 m, in the upper Río Cauca Valley and on the slopes of the Cordillera Oriental (but not in the Magdalena Valley that is occupied by the Gray-legged Night Monkey *Ao. griseimembra*), extending its range S into Ecuador through the humid subtropical forests of the Cordillera Oriental. The Lemurine Night Monkey is rather shaggy and long-haired, with the upperparts of the body often eumelanin grayish to buffy-agouti, with a poorly defined brownish medial dorsal band. The underside of the body is pheomelanin bleached yellowish to pale orange. Inner and outer sides of limbs are entirely grayish-agouti, or the inner sides have a yellowish to pale orange tone extending from the chest and belly to the mid-arm or mid-leg. Hands and feet are dark. Temporal stripes may be separated or united behind the head. From ancestral *Ao.*

*lemurinus* derived the Gray-legged Night Monkey taxon *Ao. griseimembra*. It is distributed in N Colombia and NW Venezuela. It occurs in the Río Magdalena Valley and northern lowland forests of Colombia (including the Sierra Nevada de Santa Marta and the Ríos Sinu and San Jorge basins), extending into Venezuela in the vicinity of Lake Maracaibo. It is grayish to brownish-agouti on the side of the neck. Upperparts are grayish to buffy; chest, belly, and inner surfaces of the legs are brownish or yellowish to pale orange. Pelage is relatively short. Hands and feet are light-brown. From taxon *Ao. griseimembra* derived to the NW the monotypic Panamanian Night Monkey *zonalis*. This taxon is distributed in NW Colombia in the Pacific lowlands, S towards the Ecuadorian border, and W into most of Panama; it is absent from SW Panama (Chiriquí). Its overall coat color is brownish in the Canal Zone and Colombia, but it grades into paler and grayer tones along the upper Río Tuira, E Panama. From *Ao. zonalis* derived Hernández-Camacho's Night Monkey *Ao. jorgehernandezi*. This monotypic taxon is believed to occur in the (sub)-montane tropical forests on the western slopes and foothills of the W Colombian Andes (in Quindío and Riseralda). It is advanced bleached to albinotic in the head and ventral parts. Its face has two discrete supraocular white patches separated by a broad black frontal stripe. Moreover, subocular white bands of fur are separated by a thin black malar stripe on each side of the head. Ventral parts of the arms from the wrists running up into the chest and belly are of a thick white fur (Fig. 39). From the Gray-necked Night Monkey Clade's nearest to archetypic taxon *Ao. lemurinus* derived to the SE first Brumback's Night Monkey *Ao. brumbacki*. This monotypic taxon is distributed in NC Colombia in the eastern part of Boyacá Department, E to the highlands of Meta (to at least 1,500 m above sea level). Its coat is dorsally grayish-buffy agouti colored with a dark brown mid-dorsal zone. Ventral parts extending to the elbows, knees, and lower throat are pale orange. Sides of the neck are entirely grayish or brownish agouti, like the flanks and outer sides of the arms. The head shows well-marked, thin, brownish-black temporal stripes. The white above the eyes is yellowish, and the white on the face extends to the chin. From *Ao. brumbacki* derived first to the S Spix's Night Monkey *Ao. vociferans*. This mono-

typic taxon is widespread in the upper Amazon Basin, extending from NW Brazil (W of the Negro, Uaupés, and Amazonas-Solimões Rivers) into SE Colombia (S of the Río Tomo, Orinoco Basin), and S into the Ecuadorian Amazon and NE Peru (as far south as the north bank of the Marañón-Amazonas River). It occurs also S of the Rio Solimões in a small area on the lower Rio Purús. Spix's Night Monkey's coat is brown-toned above, with an overall white, slightly orange tinged underside, extending to the wrists, ankles, and chin. Hands and feet are black. The proximal one-third to one-half of the ventral side of the tail is reddish or grayish-red, the rest is black. The crown stripes on the head are thick and brownish, with white fur above the eyes confined to two small patches grading into the agouti-colored crown. The temporal stripes are united behind, and the malar stripe can be well defined to absent. The face is white, except for the chin. From *Ao. vociferans* derived to the N and E the monotypic Humboldt's Night Monkey taxon *Ao. trivirgatus*. It is widespread across N Brazil, N of the Rios Negro and Amazonas and W of the Rio Trombetas, N into SC Venezuela and E Colombia. Sides of the neck are grayish-agouti to mainly brownish-agouti colored. Upper parts of the body are grayish to buffy-agouti. The inner sides of the limbs, extending to the wrists and ankles, are similar in color to the orange-buffy of chest and belly. The face has triradiate brown stripes. It is rather grayish in comparison with the usual white of other Night Monkeys. Hands and feet are dark-brown. Taxon *Ao. trivirgatus* can be distinguished from all other Night Monkeys by its parallel temporal stripes on the head and the lack of an interscapular whorl or crest (Figs. 45, 46).

Within the Red-necked Clade of Night Monkeys, the Black-headed Night Monkey *Ao. nigriceps* is the nearest to archetypic, less pheomelanin bleached taxon (Fig. 47). This monotypic species is distributed in the Brazilian Amazon, S of the Rio Amazonas-Solimões and W of the Rio Tapajós-Juruena, as far south as the right bank of the Rio Guaporé and the left bank of the Río Madre de Dios in N Bolivia. It occurs also in SE Peru, west to the Río Huallaga, and north as far as the Río Cushabatay. Its coat is iron-gray above and brownish-agouti on the dorsum. The underside is orange colored with white tones, extending to the neck, throat, chin, and sides of the jaw and also to the

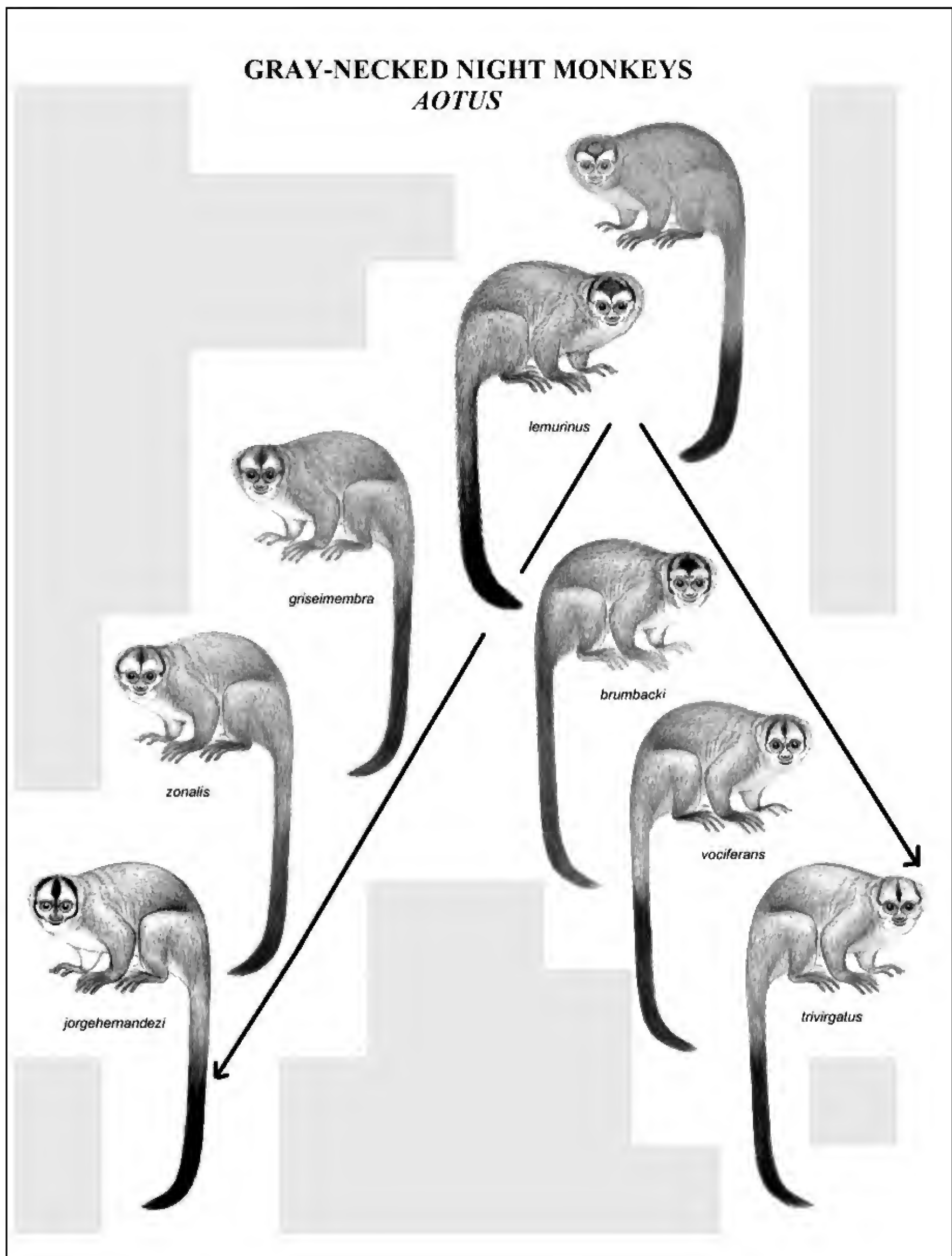


Figure 46. Radiation and metachromic diversification in the Gray-necked Night Monkey Group (*Aotus*), following eumelanin and pheomelanin pathways of metachromic bleaching, in particular in the head, proximal half of the tail, and ventral parts of the body.

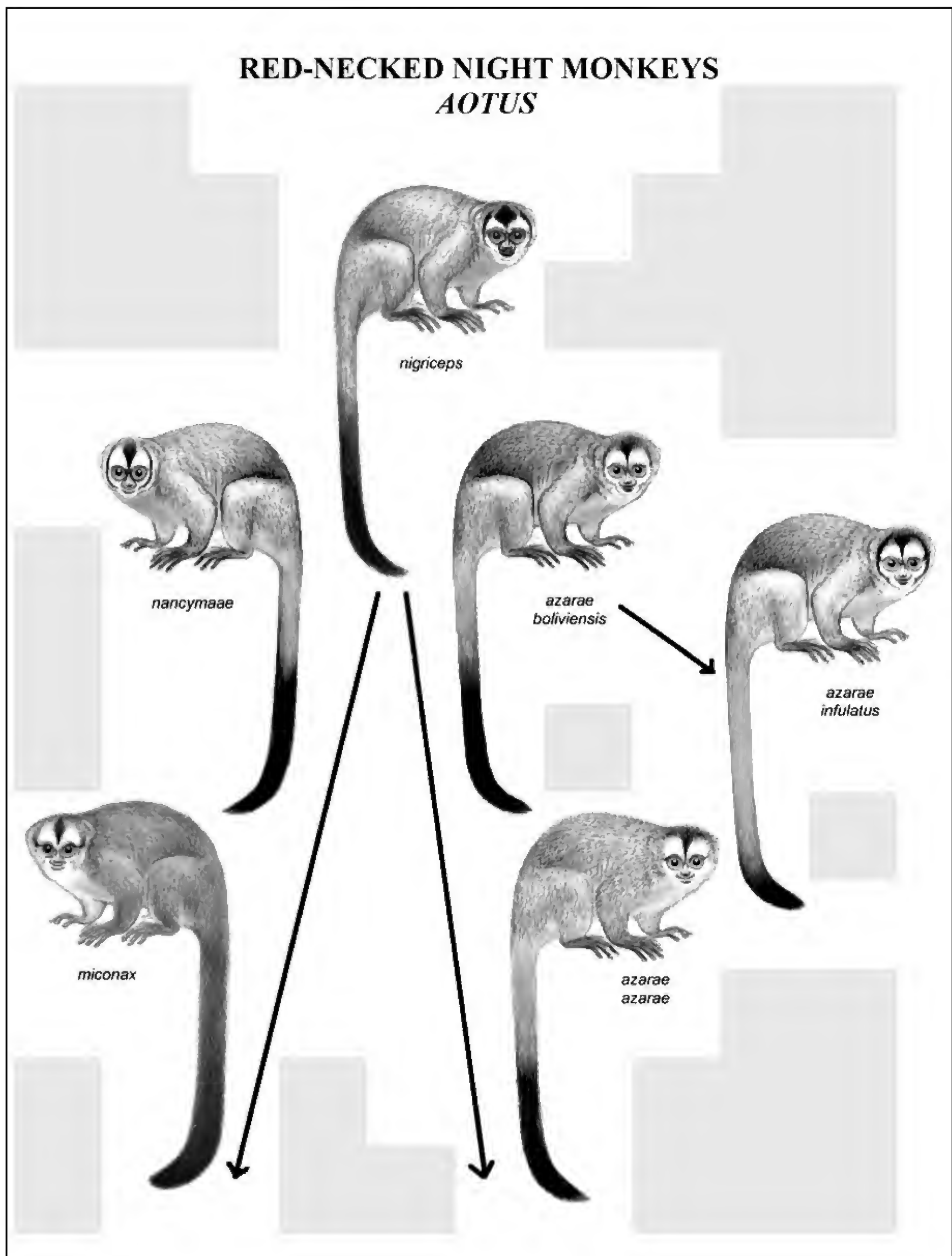


Figure 47. Radiation and metachromic diversification in the Red-necked Night Monkey Group (*Aotus*), following eu-melanin and pheomelanin pathways of metachromic bleaching, in particular in the head, tail, and ventral parts of the body.

inner surfaces of the wrists and ankles. The cap is black, the face stripes are broad, and it has distinct areas of white on the face.

From the Black-headed Night Monkey *Ao. nigriceps* derived to the W Ma's Night Monkey *Ao. nancymae*. This monotypic taxon ranges in W Brazil (S of the Rio Solimões from the Rio Javari as far east as the Rio Jandiatuba) and NE Peru (from the Rio Javari W to the Río Huallaga). This taxon is also found in an enclave between the lower Ríos Tigre and Pastaza. The upper parts of its coat are grayish-agouti, with a dark mid-dorsal zone and a pale orange underside, extending up the sides of the neck and inner limbs. The proximal part of the tail is orange, with a blackish stripe above; the underside is blackish. Its face is grayish-white, the crown stripes are narrow and dark brown colored, and the sides of the throat and jaw are colored like the body (Fig. 41). From *Ao. nancymae* derived to the W the Andean Night Monkey taxon *Ao. miconax*. This monotypic night monkey is endemic to Peru. It is confined to a small area S of the Río Marañón and W of the Río Huallaga. It inhabits the primary and secondary humid, lower-montane cloud forests in the Andes at elevations of 800–2,800 m.

Upper sides of its coat are light gray with a brownish tint, often quite infused with red-brown. Its underside is pale orange, extending forward as far as the chin and on the inner sides of the limbs. Outer surface of the body is overall brownish to buffy-agouti. The tail is bushy, its upper side is blackish, its lower side reddish-orange. Head parts and throat are advanced bleached to near-albinotic. From the nearest to archetypic Red-necked Black-headed Night Monkey *Ao. nigriceps* derived in opposite direction (to the S and E) Azara's Night Monkey species *Ao. azarae*. Three subspecies of *Ao. azarae* are recognized: the nominate taxon *Ao. azarae*, distributed in SC Brazil, S Bolivia, Paraguay, and N Argentina; taxon *Ao. boliviensis*, distributed in SE Peru and Bolivia east of the Andes; taxon *Ao. infulatus*, distributed in Brazil, S of the Rio Amazonas (but with a small enclave in the SE tip of Amapá State), including Marajó and Caviana Islands, extending east into Maranhão State as far as the Rio Parnaíba, S along the west bank of the Rio Tocantins to the Pantanal of Mato Grosso. Taxon *Ao. azarae infulatus*'s western limit is the Rio Tapajós-Juruena. Azara's Night Monkey *Ao. azarae* is highly variable. It generally has an in-

terscapular whorl. Taxon *Ao. azarae* has a long, thick, and shaggy fur that is grayish to pale buffy-agouti above and pale whitish-orange below. Facial stripes are narrow. The basal hairs of the distal ¼ of the tail are orange. Taxon *Ao. boliviensis* has a relatively short fur, with an olive tone above and contrastingly grayer on the limbs. The facial stripes are very narrow except where the middle one expands on the crown; the black temporal stripe in this taxon is poorly defined, the black malar stripe is faint or absent, and there is usually a whitish band between the eyes and temporal stripe. There is a conspicuous whorl between the shoulder blades. The third taxon *Ao. infulatus*, the "Feline Night Monkey", is very similar to subspecies *Ao. boliviensis*, but the white on the face is more prominent. There is no whitish band between the eyes and the temporal stripe as there is in *Ao. boliviensis*. The temporal stripes are black, well defined, and continuous with the malar stripe. The tail is reddish throughout its length except for the black tip. The orange color of the underparts extends to or above the ventral one-half of the sides of the neck. The color of the throat varies from orange, with the anterior one-half grayish-agouti to entirely orange colored (Fig. 47).

Our theory suggests that the trend to allopatry in Neotropical primates resulted from a specific kind of social selection. That the discrimination of somewhat deviant mutant young males by high-ranking males, which push them toward the periphery of the parental group's range, has been the true driver behind metachromic bleaching on the evolutionary path along which a certain race, species, phylogenetic clade, or genus has extended its geographic range in the past. As any founder-colony or population at the limit of a taxon's current range will represent a narrow gene pool, through inbreeding certain phenotypic characters (e.g., local depilation of the skin, change of coloration of the skin, pelage or parts of it) will initially be reinforced and advance more rapidly within the population. Through the process of metachromism (changing hair and skin color) with the trend to allopatry as the behavioral driving force, speciation, radiation, and phylogeography can be retraced and well explained for in all extant Neotropical primates. According to the principle of metachromic bleaching, extant primate taxa at the base of a phylogenetic tree or clade are in general agouti or saturated



eumelanin colored. They are the least colorful, black(ish) or dark brown toned, and therefore considered to be nearest to the ancestral, archetypic, primitive or original form.

Geographic variation and diversification in color patterns of the coat among Neotropical monkeys demonstrates with unusual clarity the unilateral direction and irreversibility of processes that lead to progressively metachromic bleached and ultimately (near)-albinotic allopatric forms, irrespective of environmental factors (Figs. 1–47). The essentially behavioral and genetic driving forces behind metachromic processes, though, have never been studied. They are generally considered enigmatic. The reason may be that they seem to disobey commonly accepted Darwinian rules of evolution. Different from birds, in territorial (Neotropical) monkeys metachromic changes in coat color toward bleaching or albinotic and/or all sorts of local hair growth or loss of hair (depilation) do not seem to play an essential role in sexual display and mate selection. Consequently, they may seem to be non-adaptive. In the wild only rarely one is able to witness how exactly processes of metachromic bleaching do work out. For instance: when somewhat bleached or depilated deviant young males are being pushed from the center into the periphery of a ranging or foraging group. Or: when ‘outcast’ males do join in all-male parties. Or: when such parties set out to look beyond the horizon, for mere survival willing to overtake any habitat delimitation or geographic barrier found on their ‘path to allopatry’. These crucial data will only come available when fieldworkers, like we did, do live for prolonged periods of time among undisturbed primate populations in pristine tropical forest environment. As very few primatologists have done so, at least in the Neotropics, and sample sizes are consequently too small to be published and divulged, it is impossible for us to add more references than our own on the matter. Even though, living over more than a decade in permanent intimate contact with pristine nature, both in the Brazilian Amazon and in the overall even better preserved Guayanan Shield, led us to believe that high-ranking males pushing slightly bleached and/or depilated young males to the periphery of a group’s range, or sometimes beyond its boundaries, could plausibly be the true and principal motor or driver behind allopatric speciation and radiation of taxa in nearly all Neotropical

primate genera - Pygmy Marmosets (*Cebuella*), Tamarins (*Saguinus*), Amazonian Marmosets (*Mico*), True Marmosets (*Callithrix*), Lion Tamarins (*Leontopithecus*), Sakis (*Pithecia*), Bearded Sakis (*Chiropotes*), Uakaris (*Cacajao*), Titi Monkeys (*Callicebus*), Night Monkeys (*Aotus*), Squirrel Monkeys (*Saimiri*), Gracile/Untufted Capuchin Monkeys (*Cebus*), Robust/Tufted Capuchin Monkeys (*Sapajus*), Howling Monkeys (*Alouatta*), Woolly Monkeys (*Lagothrix*), Spider Monkeys (*Ateles*), and Woolly Spider Monkeys (*Brachyteles*). Interestingly, but concurring with our theory (for those monkeys that do not defend a common territory), metachromic bleaching did not take place in peaceably living monkeys like the archetypic agouti and saturated eumelanin colored Black-crowned Dwarf Marmosets *Callibella humilis*, a newly identified monotypic genus of diminutive callitrichid monkeys (Figs. 2, 3). Nor did it take place in saturated eumelanin all-black Goeldi’s Monkeys (*Callimico goeldii*) - the only other monotypic primate genus in the Neotropics that does not behave territorial in any sense and therefore does not defend a common living space against the neighbors of its own kind (Fig. 4). Their external features showing archetypic agouti and saturated eumelanin coat coloration without any sign of metachromic bleaching are in full accordance with their genetics that put them at the base of their respective phylogenetic trees. It further corroborates our theory on the origin of allopatric speciation in primates and the principle of metachromic bleaching, for Dwarf Marmosets and Goeldi’s Monkeys are equally sociable, peaceable little monkeys that do not demonstrate any rate of territorial defense. The primitive agouti and saturated eumelanin (blackish-brown) Black-crowned Dwarf Marmoset stands at the base of the phylogenetic tree of all Amazonian marmosets (Van Roosmalen & Van Roosmalen, 2003). It represents the nearest to ancestral, archetypic marmoset from which all extant, advanced and highly territorial Amazonian marmosets (genus *Mico*) and pygmy marmosets (genus *Cebuella*) have derived in the Late Pleistocene.

Our theory is firmly rooted in over 30-year fieldwork on primates, both in the Guianas and in the entire lowland Amazon Basin. From the very beginning we have given special attention to issues like socio-ecology, ecological feeding niches, territorial behavior, distributions, and phylogeography.

Simultaneously, we have kept, raised, bred, rehabilitated, and reintroduced back into the wild entire families or social groupings of a multitude of monkey taxa representing about all hitherto known Neotropical primate genera. Many unique, extremely rare or sometimes once-in-a-lifetime observations that we gathered in pristine tropical rainforest environment as well as in captivity (the bulk of it never published inherent to 'insignificant' sample sizes) now do add up to the validity of our theory. It basically helps us to better understand the complex distribution patterns, phylogeography, diversification, speciation, and radiation in Neotropical primates. Most likely, the theory applies to all the world's primates (including man), as long as the taxa exhibit social groupings that defend a common living space, home range, or territory. The fact that only two Neotropical primate genera (*Callimico* and *Callibella*) are monotypic strongly supports our theory, as it does not apply to peaceable, non-territorial social primates. By boat, canoe, and on foot we have surveyed entire basins of a number of major tributaries of the mighty Amazon River to study primate diversity and distributions across the entire Amazon Basin, including also large parts of the Brazilian and Guyanan Shields. We have tested and empirically come to fully validate Alfred Russel Wallace's river-barrier hypothesis that he first laid down in his 1852 account *On the Monkeys of the Amazon*, and later in his 1876 paper "The Geographical Distributions of Animals". Herein, Wallace points at the larger rivers that he sailed as the principal evolutionary cause of the Amazon's rich extant primate diversity and complex biogeography, since many rivers effectively block off gene flow between populations along opposite riverbanks (genetic isolation). As the Amazon still represents a largely pristine and vast natural realm that is (not yet) drastically and irreversibly modified by human interference, no better place to study and retrace evolutionary processes that may have acted upon primates and other mammals since the Pliocene era, no matter on which continent. Moreover, most rivers that in the course of millions of years have played a significant role in the demography of Amazonian primates - the majority of which cannot swim or fly - remain acting as such. Therefore, distributions of primate taxa in the Amazon, if correctly studied, documented, and taxonomically treated, do follow a more transparent and rational

overall pattern in comparison with those of the Old World. In SE Asia, instead of rivers, the ocean played an equally important role in the island biogeography of mammals. And in Africa (including Madagascar), the landscape with its complex and diffuse mosaic of vegetation types and habitats seems to have played a more determinant role than rivers in primate distributions. Moreover, massive human disturbance has long irreversibly changed the landscape of the Old World. This may have obscured to some extent the principal factors that influenced and determined distributions and phylogeography in catarrhine primates, most importantly the hominins.

## CONCLUSIONS

Here we discuss the above proposed doctrine on the origin of allopatric primate species and the principle of metachromic bleaching among Neotropical primates as a conclusive socio-ecological answer to the question: why primates are such a highly diversified, species-rich, and colorful order in the Class Mammalia. The Order Primates contains a world total of 73 genera, 414 IUCN-recognized species, and 612+ known taxa of which roughly one third are found in the Neotropics (Mittermeier et al., 2013) (see also Table 1). Globally, only the rodents (Order Rodentia) outnumber the Order Primates. However, compared to primates, rodents are by far not that diversified. They are mostly opportunists, not very sociable, and not particularly colorful. While studying color variation in callitrichid monkeys, Hershkovitz (1968; 1977) proposed the "Theory of Metachromism.". He attributed evolutionary change in mammalian tegumentary colors to social, sexual, and predatory selection, as it seems to be the case in birds. He argued that the highly 'visually' adapted primates may be predisposed to select mates based on coat color and hair adornments. However, primates generally do not sexually display their skin and coat colors, or hair dresses, except for a few genera in the Old World (e.g., *Theropithecus*, *Mandrillus*). Instead, some display their genitals, like both sexes of Amazonian Marmosets (genus *Mico*) do. Or, both sexes of Bearded Sakis (*Chiropotes*), female Spider Monkeys (*Ateles*) or male Woolly Spider Monkeys (*Brachyteles*) do. In that case, their genitals are

mostly hypertrophied (e.g., *Mico*, *Chiropotes*, *Brachyteles*, *Pan*). HersHKovitz's key hypothesis of metachromism, which is tested in tamarins (genus *Saguinus*) and confirmed for many of its predictions by Jacobs et al. (1995), concerns the orderly, irreversible loss of pigment within chromogenetic fields. Its key concept is that genetic drift together with social selection could fix phenotypes departing from primitive agouti or saturated eumelanin (blackish-brown) fields by various degrees of so-called "metachromic bleaching". Thus, an albinotic (nearly white) coat would represent the end point of geographic variation in a series of near-allopatric forms (color morphs) deriving ultimately from an agouti-colored or saturated eumelanin pigmented ancestral form. Using metachromism, we have demonstrated that most Amazonian monkey genera are monophyletic and composed of two or more major phylogenetic Groups or Clades. We found only two genera (i.e., *Callibella* and *Callicimico*) to be monotypic. Contrary to HersHKovitz, who followed the Darwinian fallacy of adaptive evolution by linking evolutionary change in mammalian tegumentary colors ('bleaching') to social, sexual, and predatory selection, we suggest to attribute metachromic diversification in extant social and territorial primates exclusively and uniquely to "male social selection". We propose the "trend to allopatry in somewhat metachromic bleached and/or depilated varieties" to be the principal mechanism and driver behind speciation, radiation, and phylogeography in group-living Neotropical monkeys that defend the group's living space. It arguably applies also to any group-living territorial primate worldwide, including our own species and its ancestors (be it hominids or hominins). For all nineteen genera of Neotropical primates we have presented distribution maps of all known extant taxa and indicated the geographic barriers (rivers, lakes, mountain ranges, seasonally inundated floodplain forests, open scrub areas, etc.) delineating each taxon's distribution. We have also elaborated the phylogeography and radiation within each monophyletic cladistic Group or Clade and related them to the irreversible patterns of metachromic bleaching. Through the process of metachromism (changing hair and skin colors) with the trend to allopatry as the behavioral driving force, speciation, radiation, and phylogeography can be well retraced and explained for in all extant Neotropical primates.

According to the principle of metachromism, primate taxa at the base of a phylogenetic tree or clade are in general agouti or saturated eumelanin (black or blackish-brown) colored - that is the least colorful. Within that Clade they are considered the nearest to ancestral, archetypic, primitive, or original taxon. Based on metachromic skin and fur characters, without a single exception, we were able to retrace phylogeographic pathways of speciation and radiation that were plausibly followed in the evolutionary history of each monophyletic Clade. In all cases we could confirm the trend to allopatry following irreversible eumelanin and pheomelanin pathways of metachromic bleaching. The farther a taxon radiated away from the origin or center of the Clade's dispersion, the more progressively eumelanin or bleached and eventually albinotic its coat/pelage, or part of it, will become.

The great majority of primates are sociable, group-living animals. Group sizes vary from nuclear families (4–7 individuals) to troops of mixed age and sex classes containing 15 to over 200 individuals. The far majority of the world's primate societies are socially structured in a hierarchic way and based on male dominance and ranking. Male defense of the group and its living space within a population benefits from male social selection. Even in matriarchally organized social groups, such as those of spider monkeys (*Ateles*) and pygmy chimpanzees or bonobos (*Pan*), males associate in all-male parties to jointly patrol and defend the group's territory or living space. In social conflicts among males over ranking, inferior males as well as mutant males that show somewhat different, deviant phenotypic characters (such as a slightly bleached pelage here or there or depilated skin in certain body parts) will be pushed into the periphery of the group during ranging and foraging. We have seen this happening, both in the wild and in semi-free ranging conditions, in particular in social groups and societies of monkeys like *Lagothrix*, *Ateles*, *Cebus*, *Sapajus*, *Saimiri*, *Cacajao*, or *Chiropotes*. Depending on the species, such young males also happen to be expelled from the parental group. We have witnessed this in wild and semi-free ranging populations of *Alouatta*, *Callicebus*, *Mico*, *Cebus*, *Sapajus*, and *Pithecia*. Either way, the chances of outcast males to survive and pass on their mutant genes are utterly slim. If this would happen in other mammals - being comparatively

<p><b><i>Alouatta</i></b> Lacépède, 1799</p> <p><i>Alouatta arctoidea</i> Cabrera, 1940 <i>Alouatta belzebul</i> (Linnaeus, 1766) <i>Alouatta caraya</i> (Humboldt, 1812) <i>Alouatta discolor</i> (Spix, 1823) <i>Alouatta guariba guariba</i> (Humboldt, 1812) <i>Alouatta guariba clamitans</i> Cabrera, 1940 <i>Alouatta macconnelli</i> Elliot, 1910 <i>Alouatta nigerrima</i> Lönnberg, 1941 <i>Alouatta palliata palliata</i> (Gray, 1848) <i>Alouatta palliata aequatorialis</i> Festa, 1903 <i>Alouatta palliata coibensis</i> Thomas, 1902 <i>Alouatta palliata mexicana</i> Merriam, 1902 <i>Alouatta palliata trabeata</i> Lawrence, 1933 <i>Alouatta pigra</i> Lawrence, 1933 <i>Alouatta sara</i> Elliot, 1910 <i>Alouatta seniculus seniculus</i> (Linnaeus, 1766) <i>Alouatta seniculus juara</i> Elliot, 1910 <i>Alouatta seniculus puruensis</i> Lönnberg, 1941 <i>Alouatta ululata</i> Elliot, 1912</p> <p><b><i>Aotus</i></b> Illiger, 1811</p> <p><i>Aotus azarae azarae</i> (Humboldt, 1812) <i>Aotus azarae boliviensis</i> Elliot, 1907 <i>Aotus azarae infulatus</i> (Kuhl, 1820) <i>Aotus brumbacki</i> Hershkovitz, 1983 <i>Aotus griseimembra</i> Elliot, 1912 <i>Aotus jorgehernandezi</i> Defler et Bueno, 2007 <i>Aotus lemurinus</i> I. Geoffroy Saint-Hilaire, 1843 <i>Aotus miconax</i> Thomas, 1927 <i>Aotus nancymae</i> Hershkovitz, 1983 <i>Aotus nigriceps</i> Dollman, 1909 <i>Aotus trivirgatus</i> (Humboldt, 1811) <i>Aotus vociferans</i> (Spix, 1823) <i>Aotus zonalis</i> Goldman, 1914</p> <p><b><i>Ateles</i></b> É. Geoffroy Saint-Hilaire, 1806</p> <p><i>Ateles belzebuth</i> É. Geoffroy Saint-Hilaire, 1806 <i>Ateles chamek</i> (Humboldt, 1812) <i>Ateles fusciceps fusciceps</i> Gray, 1865 <i>Ateles fusciceps rufiventris</i> Sclater, 1872 <i>Ateles geoffroyi geoffroyi</i> Kuhl, 1820 <i>Ateles geoffroyi azuerensis</i> (Bole, 1937) <i>Ateles geoffroyi frontatus</i> (Gray, 1842) <i>Ateles geoffroyi grisescens</i> Gray, 1865 <i>Ateles geoffroyi ornatus</i> (Gray, 1870) <i>Ateles geoffroyi vellerosus</i> Gray, 1865 <i>Ateles geoffroyi yucatanensis</i> Kellogg et Goldman, 1944 <i>Ateles (hybridus) hybridus</i> I. Geoffroy Saint-Hilaire, 1829 <i>Ateles (hybridus) brunneus</i> Gray, 1870 <i>Ateles longimembris</i> Allen, 1914 <i>Ateles marginatus</i> É. Geoffroy Saint-Hilaire, 1809 <i>Ateles paniscus</i> (Linnaeus, 1758)</p>	<p><b><i>Brachyteles</i></b> Spix, 1823</p> <p><i>Brachyteles arachnoides</i> (É. Geoffroy Saint-Hilaire, 1806) <i>Brachyteles hypoxanthus</i> (Kuhl, 1820)</p> <p><b><i>Cacajao</i></b> Lesson, 1840</p> <p><i>Cacajao (calvus) calvus</i> (I. Geoffroy Saint-Hilaire, 1847) <i>Cacajao (calvus) novaesi</i> Hershkovitz, 1987 <i>Cacajao (calvus) rubicundus</i> (I. Geoffroy Saint-Hilaire et Deville, 1848) <i>Cacajao (calvus) ucayalii</i> (Thomas, 1928) <i>Cacajao (melanocephalus) melanocephalus</i> (Humboldt, 1812) <i>Cacajao (melanocephalus) ayresi</i> Boubli, Silva, Hrbek, Pontual et Farias, 2008 <i>Cacajao (melanocephalus) hosomi</i> Boubli, Silva, Hrbek, Pontual et Farias, 2008 <i>Cacajao ouakary</i> (Spix, 1823)</p> <p><b><i>Callibella</i></b> van Roosmalen M.G.M. et van Roosmalen T., 2003</p> <p><i>Callibella humilis</i> (van Roosmalen M.G.M., van Roosmalen T., Mittermeier et de Fonseca, 1998)</p> <p><b><i>Callicebus</i></b> Thomas, 1903</p> <p><i>Callicebus aureipalatii</i> Wallace, Gómez, Felton A. et Felton A.M., 2006 <i>Callicebus baptista</i> Lönnberg, 1939 <i>Callicebus barbarabrownae</i> Hershkovitz, 1990 <i>Callicebus bernhardi</i> van Roosmalen M.G.M., van Roosmalen T. et Mittermeier, 2002 <i>Callicebus brunneus</i> (Wagner, 1842) <i>Callicebus caligatus</i> (Wagner, 1842) <i>Callicebus caquetensis</i> Defler, Bueno et Garcia, 2010 <i>Callicebus cinerascens</i> (Spix, 1823) <i>Callicebus coimbrai</i> Kobayashi et Langguth, 1999 <i>Callicebus cupreus</i> (Spix, 1823) <i>Callicebus donacophilus</i> (d’Orbigny, 1836) <i>Callicebus dubius</i> Hershkovitz, 1988 <i>Callicebus hoffmannsi</i> Thomas (1908) <i>Callicebus lucifer</i> Thomas, 1914 <i>Callicebus lugens</i> (Humboldt, 1812) <i>Callicebus medemi</i> Hershkovitz, 1963 <i>Callicebus melanochir</i> (Wied-Neuwied, 1820) <i>Callicebus modestus</i> Lönnberg, 1939 <i>Callicebus moloch</i> (Hoffmannsegg, 1807) <i>Callicebus nigrifrons</i> (Spix, 1823) <i>Callicebus oenanthe</i> Thomas, 1924 <i>Callicebus olallae</i> Lönnberg, 1939 <i>Callicebus ornatus</i> (Gray, 1866) <i>Callicebus pallescens</i> Thomas, 1907 <i>Callicebus personatus</i> (É. Geoffroy Saint-Hilaire, 1812) <i>Callicebus purinus</i> Thomas, 1927 <i>Callicebus regulus</i> Thomas, 1927</p>
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Table 1/1. References of scientific descriptions of all known Neotropical primates (present paper).

<p><i>Callicebus stephennashi</i> van Roosmalen M.G.M., van Roosmalen T. et Mittermeier, 2002</p> <p><i>Callicebus torquatus</i> (Hoffmannsegg, 1807</p> <p><i>Callicebus vieirai</i> Gualda-Barros, Nascimento et Amaral, 2012</p> <p><b><i>Callimico</i></b> Miranda Ribeiro, 1912</p> <p><i>Callimico goeldii</i> (Thomas, 1904)</p> <p><b><i>Callithrix</i></b> Erxleben, 1777</p> <p><i>Callithrix aurita</i> (É. Geoffroy Saint-Hilaire, 1812)</p> <p><i>Callithrix flaviceps</i> (Thomas, 1903)</p> <p><i>Callithrix geoffroyi</i> (Humboldt, 1812)</p> <p><i>Callithrix jacchus</i> (Linnaeus, 1758)</p> <p><i>Callithrix kuhlii</i> Coimbra-Filho, 1985</p> <p><i>Callithrix penicillata</i> (É. Geoffroy Saint-Hilaire, 1812)</p> <p><b><i>Cebuella</i></b> Gray, 1865</p> <p><i>Cebuella (pygmaea) pygmaea</i> (Spix, 1823)</p> <p><i>Cebuella (pygmaea) niveiventris</i> Lönnberg, 1940</p> <p><b><i>Cebus</i></b> Erxleben, 1777</p> <p><i>Cebus aequatorialis</i> Allen, 1914</p> <p><i>Cebus albifrons</i> (Humboldt, 1812)</p> <p><i>Cebus brunneus</i> Allen, 1914</p> <p><i>Cebus capucinus capucinus</i> (Linnaeus, 1758)</p> <p><i>Cebus capucinus curtus</i> Bangs, 1905</p> <p><i>Cebus cesarae</i> Hershkovitz, 1949</p> <p><i>Cebus cuscinus</i> Thomas, 1901</p> <p><i>Cebus imitator</i> Thomas, 1903</p> <p><i>Cebus kaapori</i> Queiroz, 1992</p> <p><i>Cebus leucocephalus</i> Gray, 1865</p> <p><i>Cebus malitiosus</i> Elliot, 1909</p> <p><i>Cebus olivaceus olivaceus</i> Schomburgk, 1848</p> <p><i>Cebus olivaceus castaneus</i> I. Geoffroy Saint-Hilaire, 1851</p> <p><i>Cebus unicolor</i> Spix, 1823</p> <p><i>Cebus versicolor</i> Pucheran, 1845</p> <p><i>Cebus yuracus</i> Hershkovitz, 1949</p> <p><b><i>Chiropotes</i></b> Lesson, 1840</p> <p><i>Chiropotes albinasus</i> (I. Geoffroy Saint-Hilaire et Deville, 1848)</p> <p><i>Chiropotes chiropotes</i> (Humboldt, 1812)</p> <p><i>Chiropotes sagulatus</i> (Traill, 1821)</p> <p><i>Chiropotes satanas</i> (Hoffmannsegg, 1807)</p> <p><i>Chiropotes utahickae</i> Hershkovitz, 1985</p> <p><b><i>Lagothrix</i></b> É. Geoffroy Saint-Hilaire, 1812</p> <p><i>Lagothrix (cana) cana</i> (É. Geoffroy Saint-Hilaire, 1812)</p> <p><i>Lagothrix (cana) tschudii</i> Pucheran, 1857</p> <p><i>Lagothrix (lagotricha) lagotricha</i> (Humboldt, 1812)</p>	<p><i>Lagothrix (lagotricha) lugens</i> Elliot, 1907</p> <p><i>Lagothrix poeppigii</i> Schinz, 1844</p> <p><b><i>Leontopithecus</i></b> Lesson, 1840</p> <p><i>Leontopithecus caissara</i> Lorini et Persson, 1990</p> <p><i>Leontopithecus chrysomelas</i> (Kuhl, 1820)</p> <p><i>Leontopithecus chrysopygus</i> (Mikan, 1823)</p> <p><i>Leontopithecus rosalia</i> (Linnaeus, 1766)</p> <p><b><i>Mico</i></b> Lesson, 1840</p> <p><i>Mico acariensis</i> (van Roosmalen M.G.M., van Roosmalen T., Mittermeier et Rylands, 2000)</p> <p><i>Mico argentatus</i> (Linnaeus, 1771)</p> <p><i>Mico chrysoleucos</i> (Wagner, 1842)</p> <p><i>Mico emiliae</i> (Thomas, 1920)</p> <p><i>Mico humeralifer</i> (É. Geoffroy Saint-Hilaire, 1812)</p> <p><i>Mico intermedius</i> (Hershkovitz, 1977)</p> <p><i>Mico leucippe</i> Thomas, 1922</p> <p><i>Mico manicorensis</i> (van Roosmalen M.G.M., van Roosmalen T., Mittermeier et Rylands, 2000)</p> <p><i>Mico marcai</i> (Alperin, 1993)</p> <p><i>Mico mauesi</i> (Mittermeier, Schwarz et Ayres, 1992)</p> <p><i>Mico melanurus</i> (É. Geoffroy Saint-Hilaire, 1812)</p> <p><i>Mico nigriceps</i> (Ferrari et Lopes, 1992)</p> <p><i>Mico rondoni</i> Ferrari, Sena, Schneider et Silva, 2010</p> <p><i>Mico saterei</i> (Silva et Noronha, 1998)</p> <p><b><i>Oreonax</i></b> Thomas, 1927</p> <p><i>Oreonax flavicauda</i> (Humboldt, 1812)</p> <p><b><i>Pithecia</i></b> Desmarest, 1804</p> <p><i>Pithecia aequatorialis</i> Hershkovitz, 1987</p> <p><i>Pithecia albicans</i> Gray, 1860</p> <p><i>Pithecia (irrorata) hirsuta</i> Spix, 1823</p> <p><i>Pithecia (irrorata) irrorata</i> Gray, 1842</p> <p><i>Pithecia (irrorata) vanzolinii</i> Hershkovitz, 1987</p> <p><i>Pithecia (monachus) milleri</i> Allen, 1914</p> <p><i>Pithecia (monachus) monachus</i> (É. Geoffroy Saint-Hilaire, 1812)</p> <p><i>Pithecia (monachus) napensis</i> Lönnberg, 1938</p> <p><i>Pithecia (pithecia) pithecia</i> (Linnaeus, 1766)</p> <p><i>Pithecia (pithecia) chrysocephala</i> I. Geoffroy Saint-Hilaire, 1850</p> <p><i>Pithecia (pithecia) lotichiusi</i> Mertens, 1925</p> <p><b><i>Saguinus</i></b> Hoffmannsegg, 1807</p> <p><i>Saguinus bicolor</i> (Spix, 1823)</p> <p><i>Saguinus fuscicollis fuscicollis</i> (Spix, 1823)</p> <p><i>Saguinus fuscicollis avilapiresi</i> Hershkovitz, 1966</p> <p><i>Saguinus fuscicollis cruzlimai</i> Hershkovitz, 1966</p>
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Table 1/2. References of scientific descriptions of all known Neotropical primates (present paper).



<i>Saguinus fuscicollis mura</i> Röhe, Silva Jr., Sampaio et Rylands, 2009	<i>Saguinus weddelli crandalli</i> Hershkovitz, 1966
<i>Saguinus fuscicollis primitivus</i> Hershkovitz, 1977	<i>Saguinus weddelli melanoleucus</i> (Miranda Ribeiro, 1912)
<i>Saguinus fuscus</i> (Lesson, 1840)	<b><i>Saimiri</i></b> Voigt, 1831
<i>Saguinus geoffroyi</i> (Pucheran, 1845)	
<i>Saguinus illigeri</i> (Pucheran, 1845)	<i>Saimiri boliviensis boliviensis</i> (L. Geoffroy Saint-Hilaire et de Blainville, 1834)
<i>Saguinus (imperator) imperator</i> (Goeldi, (1907)	<i>Saimiri boliviensis peruviansis</i> Hershkovitz, 1984
<i>Saguinus (imperator) subgriseus</i> (Lönnerberg, 1940)	<i>Saimiri (cassiquiarensis) cassiquiarensis</i> (Lesson, 1840)
<i>Saguinus inustus</i> (Schwarz, 1951)	<i>Saimiri (cassiquiarensis) albigena</i> (von Pusch, 1942)
<i>Saguinus labiatus labiatus</i> (É. Geoffroy Saint-Hilaire, 1812)	<i>Saimiri macrodon</i> Elliot, 1907
<i>Saguinus labiatus rufiventer</i> (Gray, 1843)	<i>Saimiri oerstedii oerstedii</i> (Reinhardt, 1872)
<i>Saguinus labiatus thomasi</i> (Goeldi, 1907)	<i>Saimiri oerstedii citrinellus</i> (Thomas, 1904)
<i>Saguinus lagonotus</i> (Jiménez de la Espada, 1870)	<i>Saimiri (sciureus) sciureus</i> (Linnaeus, 1758)
<i>Saguinus leucogenys</i> (Gray, 1865)	<i>Saimiri (sciureus) collinsi</i> Osgood, 1916
<i>Saguinus leucopus</i> (Günther, 1876)	<i>Saimiri ustus</i> (L. Geoffroy Saint-Hilaire, 1843)
<i>Saguinus martinsi martinsi</i> (Thomas, 1912)	<i>Saimiri vanzolinii</i> Ayres, 1985
<i>Saguinus martinsi ochraceus</i> Hershkovitz, 1966	
<i>Saguinus midas</i> (Linnaeus, 1758)	<b><i>Sapajus</i></b> Kerr, 1792
<i>Saguinus mystax mystax</i> (Spix, 1823)	
<i>Saguinus mystax pileatus</i> (L. Geoffroy Saint-Hilaire et Deville, 1848)	<i>Sapajus apella apella</i> (Linnaeus, 1758)
<i>Saguinus mystax pluto</i> (Lönnerberg, 1926)	<i>Sapajus apella margaritae</i> (Hollister, 1914)
<i>Saguinus niger</i> (É. Geoffroy Saint-Hilaire, 1803)	<i>Sapajus cay</i> (Illiger, 1815)
<i>Saguinus nigrifrons</i> (L. Geoffroy Saint-Hilaire, 1850)	<i>Sapajus flavius</i> (Schreber, 1774)
<i>Saguinus nigricollis nigricollis</i> (Spix, 1823)	<i>Sapajus libidinosus</i> (Spix, 1823)
<i>Saguinus nigricollis graellsii</i> (Jiménez de la Espada, 1870)	<i>Sapajus macrocephalus</i> (Spix, 1823)
<i>Saguinus nigricollis hernandezi</i> Hershkovitz, 1982	<i>Sapajus nigrurus</i> (Goldfuss, 1809)
<i>Saguinus oedipus</i> (Linnaeus, 1758)	<i>Sapajus robustus</i> (Kuhl, 1820)
<i>Saguinus tripartitus</i> (Milne-Edwards, 1878)	<i>Sapajus xanthosternos</i> (Wied-Neuwied, 1826)
<i>Saguinus weddelli weddelli</i> (Deyville, 1849)	

Table 1/3. References of scientific descriptions of all known Neotropical primates (present paper).

less intelligent, sensitive, and sociable than primates in general are - being forced to live as outcasts would equal a sure death. But, if it were healthy male individuals deviant from the socially selected skin and/or hair color pattern that are discriminated against merely for being slightly depilated or having its coat somewhat bleached somewhere, such young males pushed out of the group's core area by high-ranking males will ally for the sake of survival alone. Their shared forced-upon marginality could well drive them into looking beyond the horizon and together leaving the pack in search of a living space wherever it could be found. Once that living condition is fulfilled, they can start a new social group incorporating some females that they were able to attract from other resident groups on their way out. This phenomenon is known to commonly take place in hierarchically structured primate societies that are ruled and defended by dominant (alpha)-males (e.g., *Alouatta*). It guarantees a certain primate to reach optimal densities in un-

disturbed populations. Furthermore, it selects for males that are capable to lead and defend a social group. All-male parties of slightly eumelanin and/or pheomelanin bleached, or somewhat depilated males that are pushed out of their parental group's living space and that follow the 'trend to allopatry', will range further and further away from the core of a taxon's distribution. If suitable habitat to settle down is not encountered, the animals eventually will weaken, suffer from diseases, starve to death, or get predated upon. Very rarely, they happen to venture into for that species marginal or unsuitable habitat, being forced to adapt to an alien habitat or a different feeding niche. In extremely rare cases, such founder-groups or -colonies may diverge along this path into a different subspecies (whatever that may be) and eventually into a different species (whatever that may be) or ecospecies. This kind of sympatric speciation may have taken place in such cases as the cream-white, near-albinotic fair woolly monkey living year-round in the várzeas between

the lower Rio Javará and the right bank of the upper Rio Solimões. Or, the pheomelanin bleached, overall orange-colored woolly monkey from the headwaters of the Rio Jutáí. Somewhat metachromic bleached founder-colonies of woollies driven by the 'trend to allopatry' once must have diverged from archetypic agouti-colored or saturated eumelanin ancestral *La. poeppigii* while adapting to a different ecological niche that was new to woolly monkeys - in this case that of a frugivorous, canopy-dwelling, brachiating inhabitant of white-water inundated floodplain forest (várzea). During our systematic surveys of primate distribution and diversity carried out in the matrix terra firme rain forest that stretches out behind the floodplain of some white-water rivers (e.g., Javará, Juruá, Purús, Madeira), we were not able to detect any differences in phenotype between individual monkeys of a given taxon that we observed along the entire course (from source to headwaters) of each of these far-apart rivers. Contrary to what is the common presumption among primatologists, this would mean that in territorial monkeys such as pygmy marmosets or saddle-back tamarins that occupy large distributions delineated by some of the largest tributaries of the Amazon, phenotypic characters of skin and pelage coloration, and/or local hair growth or depilation, seem to have stabilized across their entire distributions. In other words, within the distribution of a given Amazonian monkey there does not exist something like a gradient of slightly different phenotypes, color forms, morphs, or races. These observations from the larger field have led us attributing full-species status to primate taxa like *Cebuella pygmaea* and *C. niveiventris* that are phenotypically stable throughout their (sometimes huge) distributions. Consequently, we here introduced the concept of eco-species. This concept is firmly corroborated by the here proposed theory on the origin of allopatric primate species. An ecospecies may be best defined as: "A genetically isolated population or group of populations of a kind that does not undergo gene flow from adjacent populations of one or more closely related kinds; and that shows a stabilized phenotype across the entire range in which it occupies a well-defined ecological niche, which it defends against any outside competitor, even beyond generic level." This eco-species concept (ESC) avoids the often confusing arbitrary distinction between species, subspecies, race,

morph, or form, for it adds sociobiological restrictions to environmental (geographic, geomorphological and phytosociological) ones that use to act on speciation and radiation in sociable territorial primates. Defined as such, the ESC may apply also to similarly socially structured mammals like coatis, peccaries, and some canids. In accordance to this definition, an enclave population of *Callibella humilis* that lives year-round in igapó forest fringing the Rio Atininga - genetically isolated from the main population that lives at least one hundred km to the north in primary terra firme rain forest - should be assigned a different species name in its own right. Or, in case the ranges of two Saddle-back Tamarins of the *S. fuscicollis* Clade, hitherto being treated as subspecies, are only separated by a narrow contact zone - where its aggressive territorial defense effectively impedes any gene flow through cross-breeding or hybridization - each population should be given valid species status. But, wherever a former distributional boundary between two such ecospecies has been disrupted, removed by a vicariance, or overtaken by the more aggressive or opportunistic of two ecospecies, the latter will expand its distribution to the cost of the other. Then, a process of replacement is set in motion along a steadily moving frontline, which inevitably will lead to the extinction of the less aggressive, more vulnerable, or more sensitive of the two ecospecies. According to our doctrine of allopatric primate speciation this will always be the ecospecies that is the more advanced metachromic bleached one. Here we have mentioned at least four cases across the Amazon where such process of replacement (through physical extermination) of one primate by another is ongoing or about to be terminated: 1) the archetypic agouti, gray, and dark red-brown coated Lake Baptista Titi Monkey *Callicebus baptista* extending its range along the southbank of the Rio Amazonas to the cost of the advanced bleached, yellow- and-gray coated Hoffmanns's Titi Monkey *Callicebus hoffmannsi* and the near-albinotic eco-species from the right bank of the Rio Mamurú; 2) the archetypic saturated eumelanin Midas Tamarin *Saguinus midas* versus the progressively bleached, halfway to fully albinotic Pied Two-colored Tamarin *S. bicolor* (including *S. ochraceus*) and Martins's Bare-face Tamarin *S. martinsi*, the latter three ecospecies being currently at the verge of extinction caused by a rapid southern expansion of midas

(Fig. 10); 3) the saturated eumelanin Weddell's Saddle-back Tamarin *S. (fuscicollis) weddelli* expanding its range to the cost of the near-albinotic Rondon's Marmoset *Mico rondoni*, pushing the frontline eastward into the interfluvium delineated by the Rios Guaporé and Jí-Paraná after having traversed the upper Rio Madeira in the recent past; 4) Gray's Saki *Pithecia hirsuta* (or *P. mittermeieri*) extending its range northwards to the cost of the near-albinotic Buffy Saki taxon *P. albicans*. In cases of replacement it is always the more advanced metachromic bleached to albinotic ecospecies that is losing the battle and eventually will go extinct. Though only documented by us in semi-captive and free-ranging, but artificially composed multi-species populations, during social conflicts it was invariably the more advanced metachromic bleached individual monkey or group of monkeys that suffered from dominant-male discriminatory behavior, being bullied, repeatedly physically attacked or violently assaulted, and eventually forced out of the core (compound) area, where we provided additional food on feeding platforms constructed up in the canopy. If not moving voluntarily to the periphery, so turning into outcasts, these monkeys could be bitten to death by the invariably less bleached, more aggressive, conspecific leading male(s). In retrospect, we recall that all neotonic, advanced metachromic bleached and near-albinotic individual monkeys kept free-ranging in our respective halfway-houses by comparison were invariably more soft-hearted, more sensitive, cooperative, adaptable, and (not surprisingly?) smarter than the male congeners by whom they were discriminated, pushed into the periphery, or banned from the core area. Applying these observations to the wild, the trend to allopatry boosted by seemingly non-adaptive social selection - leading males that discriminate upon phenotypically deviant mutant young males - in evolutionary sense could well turn out to be truly adaptive. To cite Charles Darwin (1859): "*In the long history of humankind -and animalkind, too- those who learned to collaborate and improvise most effectively have prevailed*". And: "*It is not the strongest of the species that survives, or the most intelligent that survives. It is the one that is the most adaptable to change.*"

Applying the doctrine to the evolution of hominins, in particular *Homo sapiens*, one may ponder and speculate about questions like the following:

*"Why, and driven by what force about six million years ago somewhere in Tropical Africa an ape-like lineage of primates -our hominid ancestors- left the rain-forest canopy and ventured into an arid open-savanna scrub landscape?"*

The common ancestors of the Great Apes and the human line of hominins (*Homo*) were arboreal primates that had adopted brachiation (suspended arm-over-arm-swinging underneath the twig/branch substrate) as a special locomotor pattern. Brachiation allows large-bodied arboreal primates to quickly move through the canopy and get to the fleshy fruits that are, as is the rule in any tropical rain-forest environment, distributed in the far periphery (small-branch/twig micro-habitat) of canopy- and emergent-tree tops. Brachiation is a primarily arboreal type of locomotion that evolved exclusively in some Neotropical Monkeys (i.e., spider, woolly and woolly spider monkeys) as well as in the Old-World Apes (i.e., gibbons, siamangs, bonobos/pygmy chimps, chimpanzees, orang-utans, and gorillas). It may never have evolved in Prosimians, which are the more primitive among all the world's primates. It followed an independent evolutionary path, a convergent or parallel evolution, in a physiognomically similar natural environment - the tropical forests of Southeast Asia, Central Africa, and South America (the larger Amazon Basin). A major intercontinental difference is that some monkeys in the Neotropics developed a prehensile tail as extra support in suspensory locomotion, therefore called "semi-brachiation", whereas apes during the evolutionary process toward brachiation lost a functional tail. Brachiation without use of a fifth limb is called "true brachiation". Most plausibly, our early ape-like hominid ancestors that about 6 MYA descended from the canopy of Central-African rain forest much resembled extant Spider Monkeys in their general locomotor pattern and diet. Brachiation is associated with a dietary preference for ripe, pulpy, nutritious fruits that contain a single to few large seeds. The upright position of the trunk associated with an arboreal life-style involving much brachiation happened to be a crucial pre-adaptation for later bipedal (two-legged) upright walking on the ground. It enabled our early ancestors to leave the trees in the same way as gorillas once did, but different in that the Great Apes adopted 'knuckle-walking' as the principal locomotor pattern to walk on the ground.

Similarities between Spider Monkeys and Chimpanzees are striking as we consider that at least twenty-five million years of evolution on different continents do separate these primates from one another. Cognitive features that both brachiating primates share are the mental capacity to visualize, pre-plan, and map out in time and space complex economic foraging routes to be followed that very day, tomorrow, the day after tomorrow, and perhaps even over several days ahead. Moreover, these primates are able to lay out these foraging routes across a landscape that is covered with dense tropical rain forest containing only few seasonal, widely dispersed food sources at any given time (Van Roosmalen, 1985a; 2013a). Consequently, both spider monkeys and pygmy chimpanzees (bonobos) may well depict a marked period or stage in the evolution of our early ancestors that may have specialized first in feeding upon ripe, juicy, lipid- and protein-rich, large-seeded fruits. Perhaps, that feeding niche may have been the condition that predestined our ancestors, both locomotorily and mentally, to leave the trees and become two-legged ground-dwelling foragers with an advanced use of the hands (e.g., dexterity, precision grips, tool-fashioning). And at the same time growing big babies and three to four times bigger brains (Lynch & Granger, 2008). In physical, anatomical, physiological, and mental respect, therefore, descending from the trees and adapting locomotorily to bipedal walking and running over the ground was not the 'near-impossible' step that it may seem to be. If we put it in Darwinian evolutionary perspective, however, to let it happen, until now an intraspecific social driver was missing that must have acted on the undoubtedly territorially and hierarchically organized communities of these ape-like ancestors with the brain size of contemporary chimpanzees (400 cc). Forthcoming our thirty-five years living in the Amazon and conducting long-term research on captive, feral, as well as wild monkeys - the latter mostly representing pristine populations that were never in any way disturbed by humans - we here suggest the 'trend to allopatry' among slightly depilated and/or metachromic bleached male individuals (mutants) in primate populations being the principal force that has driven founder-colonies of our early ancestors - for the mere sake of survival - out of their preferred habitat - canopy trees - into (to them) new, with respect to natural enemies risky

and hostile landscapes. As sociable and intelligent mammals suffering from intraspecific population pressures and discriminatory social constraints, outcast males must have taken on the challenge to traverse whatever barrier on their way out. So, they ventured into the arid, in many aspects hostile natural environment of savanna scrub and open woodlands. In a similar way as a small population of Gracile Capuchins on the slopes of tepuís like *Pico da Neblina* successfully adapted to a predominantly ground-dwelling life-style; the Mountain *Gorilla* successfully adapted to a fully terrestrial life-style in the cloud forests of the Virunga volcanoes in Central Africa; the Western Chimpanzee of the 'subspecies' *verus* once adapted to a predominantly terrestrial life-style in an arid, for specialist frugivores inappropriate or marginal natural environment - the open savanna scrub of West Africa (Patterson et al., 2006); the near-albinotic Rio Javari Fair Woolly Monkey with an overall cream-white colored coat, and the Rio Jutai Orange Woolly Monkey with an overall orange colored coat, adapted to várzea floodplain forest along the upper Amazon and lower Javari Rivers, and the upper Jutai River, respectively; the Peruvian Yellow-tailed Woolly Monkey in complete isolation adapted to high-altitude cloud forest in the NE Peruvian Andes; the advanced pheomelanin to near-albinotic Bald-headed Uakaris adapted to seasonally inundated white-water floodplain forest (várzea) along the Amazon River and some of its southern tributaries that drain the southeastern flanks of the Andes; among others. Looking at the distribution of Central-American spider monkeys of the *Ateles geoffroyi* Clade, we could speculate about an imaginary evolutionary path that could have been followed by an advanced metachromic bleached, near-albinotic founder-colony of the Central American Yucatán Spider Monkey *Ateles (geoffroyi) yucatanensis* from the tropical forest of Yucatán Peninsula in SE Mexico. By the 'trend to allopatry' forced out of the canopy of a semi-deciduous rain forest somewhere on the Yucatán Peninsula - the taxon's current deadend distribution - some founder-colony may venture into the savanna and desert scrub of SE Mexico and from there further into the Midwest of the US. To survive in such (for spider monkeys) alien landscape it would quickly have to lose a functional tail and adopt bipedal upright walking as its main locomotor pattern. It is tempting

to imagine a similar scenario for progressively metachromic bleached, depilated, red- or white-skinned near-albinotic early hominids 6 MYA radiating away from their archetypic, saturated-eumelanin congeners they had in common with ancestral chimpanzees. Driven by the trend to allopatry, in a similar way founder-colonies may have left the semi-deciduous rain forests of C Africa and ventured first into the savannas, plains and desert scrub of N Africa and, thereafter, into the temperate-clime dominated landscape of S+C Europe, the Middle East and SE Asia. Recent evidence from molecular biology suggests that it took several hundreds of thousands years for our early ancestors to evolve in two distinct animals: the open savanna explorers leading toward proto-humans, and those remaining arboreal resulting in chimpanzees (Patterson et al., 2006). In accordance with recent phylogenetic research, the modern Chimpanzee *Pan troglodytes* diverged from the proto- or archetypic, saturated eumelanin, overall blackish-brown colored Bonobo (Pygmy Chimpanzee) *Pan paniscus*. The common Chimpanzee is an opportunist having an omnivorous diet, whereas the Bonobo holds a predominantly specialist frugivorous diet. In comparison to common Chimpanzees, Bonobos are egalitarian, peaceable, non-violent creatures that live in loosely organized, matriarchal social groups in which the males may defend their territories, but rather adopt a "Make Love No War" philosophy of life. Bonobos have never been reported to involve in raids on neighboring group males, whereas common chimpanzees have been seen performing a kind of troop-hunting culture in which beta-males led by one alpha-male sometimes do attack neighboring males or small mixed parties, killing and eating some of them. Bonobos live in the dense tropical rain forests of Central Congo. Their distribution is thought to represent the cradle of chimpanzee evolution or the center of chimpanzee (genus *Pan*) dispersion. Applying Hershkovitz' hypothesis of metachromism, Chimpanzees may well have derived from (proto)-Bonobos. Nowadays, the two species are allopatric. The trend to allopatry may have forced ancestral chimpanzees to swim across or circumvent the Congo River that does act as a geographic barrier in present-day distributions. The farther in any but southern direction from the center of *Pan troglodytes* dispersion, located just north of the Congo River, the more arid the

landscape becomes, the more often chimps do descend from the trees and 'knuckle-walk' on the ground, and the more chimps have adapted to what bonobos would consider inappropriate or marginal habitat - unsuitable to highly specialized mature fruit-eaters that bonobos are. At the same time, we see chimpanzees becoming more pheomelanin to euchromic bleached, their skin getting lighter colored (less pigmented), their coat thinner and locally depilated or almost hairless, and elderly individuals becoming gray with age.

Another question to ponder about with the doctrine in mind: "*Why, and driven by what force some of our Homo ancestors between 100,000 and 50,000 years ago left the origin and center of hominid dispersion -Central and North Africa being considered the cradle of human evolution- to venture into the clime- and habitat-wise new, but unsuitable or (at least) marginal landscape of Europe, the Middle East and Asia?*"

After *Homo erectus* having grown much bigger brains on the plains, some millions of years later the trend to allopatry may have been again the principal driving force for some founder-colonies of *Homo sapiens* to move 'Out of Africa'. The pioneers that ventured into new landscapes to the north could do so only by occupying an ecological feeding niche that was new to former small-game hunter-fisher-gatherers, that of big-game hunter-gatherers. Hereby, the invention to first carrying along fire, soon followed by the skill to kindle it, was essential in the adaptation process to a new feeding niche, as their (our) digestive system is not apt to decompose raw meat. It has to be cooked or barbecued. Apparently, in very low densities - recent estimates place the population of Europe 30,000 years ago at about 5,000 people - these humans following herds of prehistoric megafauna (e.g., mammoth) and driving them to extinction in the Holocene, have spread rapidly across the whole of Europe and Southeast Asia, one route taking them as far as Australia and Tasmania, the other to the far northeastern corner of Siberia. From these places they eventually could reach and inhabit some Pacific Islands, and most amazingly also the continent of South America, first about 30-40,000 years ago by bordering the Antarctic during one of the glacials, and a second time, about 15,000 years ago, via Beringia and North America (Van Roosmalen, 2013c). We could ask ourselves if these all could have been advanced



metachromic bleached, euchromic to albinotic founder-colonies or colonizing parties that were pushed out from dead-end distributions in Africa and Asia following the male-territorial primate-born trend to allopatry?

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